

# UNIVERSITY OF BIRMINGHAM

University of Birmingham  
Research at Birmingham

## Interactive climate factors restrict future increases in spring productivity of temperate trees

Zohner, Constantin; Mo, Lidong; Pugh, Thomas; Bastin, Jean-Francois; Crowther, Thomas

### License:

Other (please specify with Rights Statement)

### Document Version

Peer reviewed version

### Citation for published version (Harvard):

Zohner, C, Mo, L, Pugh, T, Bastin, J-F & Crowther, T 2020, 'Interactive climate factors restrict future increases in spring productivity of temperate trees', *Global Change Biology*.

[Link to publication on Research at Birmingham portal](#)

### General rights

Unless a licence is specified above, all rights (including copyright and moral rights) in this document are retained by the authors and/or the copyright holders. The express permission of the copyright holder must be obtained for any use of this material other than for purposes permitted by law.

- Users may freely distribute the URL that is used to identify this publication.
- Users may download and/or print one copy of the publication from the University of Birmingham research portal for the purpose of private study or non-commercial research.
- User may use extracts from the document in line with the concept of 'fair dealing' under the Copyright, Designs and Patents Act 1988 (?)
- Users may not further distribute the material nor use it for the purposes of commercial gain.

Where a licence is displayed above, please note the terms and conditions of the licence govern your use of this document.

When citing, please reference the published version.

### Take down policy

While the University of Birmingham exercises care and attention in making items available there are rare occasions when an item has been uploaded in error or has been deemed to be commercially or otherwise sensitive.

If you believe that this is the case for this document, please contact [UBIRA@lists.bham.ac.uk](mailto:UBIRA@lists.bham.ac.uk) providing details and we will remove access to the work immediately and investigate.

1 **Interactive climate factors restrict future increases in spring productivity of temperate**  
2 **trees**

3

4 Authors: Constantin M. Zohner<sup>1\*</sup>, Lidong Mo<sup>1+</sup>, Thomas A.M. Pugh<sup>2,3</sup>, Jean-Francois Bastin<sup>1</sup>,  
5 and Thomas W. Crowther<sup>1</sup>

6

7 **Affiliations:**

8 <sup>1</sup>Institute of Integrative Biology, ETH Zurich (Swiss Federal Institute of Technology),  
9 Universitätsstrasse 16, 8092 Zurich, Switzerland

10 <sup>2</sup>School of Geography, Earth and Environmental Sciences, University of Birmingham,  
11 Edgbaston, Birmingham, B15 2TT, UK

12 <sup>3</sup>Birmingham Institute of Forest Research, University of Birmingham, Edgbaston, Birmingham,  
13 B15 2TT, UK

14

15 \*Author for correspondence: [constantin.zohner@t-online.de](mailto:constantin.zohner@t-online.de)

16 <sup>+</sup>Constantin M. Zohner and Lidong Mo should be considered joint first author

17

18

19

20

21

22

23

24

25

26

27 **Abstract**

28 Climate warming is currently advancing spring leaf-out of temperate trees, enhancing net  
29 primary productivity (NPP) of forests. However, it remains unclear whether this trend will  
30 continue, preventing for accurate projections of ecosystem functioning and climate feedbacks.  
31 Several eco-physiological mechanisms have been proposed to regulate the timing of leaf  
32 emergence in response to changing environmental cues, but the relative importance of those  
33 mechanisms remains unclear. Here, we use 727,401 direct phenological observations of  
34 dominant European forest trees to examine the dominant controls on leaf-out. Using the  
35 emerging mechanisms, we forecast future trajectories of spring arrival and evaluate the  
36 consequences for forest carbon dynamics. By representing hypothesized relationships with  
37 autumn temperature, winter chilling, and the timing of spring onset we accurately predicted  
38 reductions in the advance of leaf-out. There was a strong consensus between our empirical  
39 model and existing process-based models, revealing that the advance in leaf-out will not exceed  
40 2 weeks over the rest of century. We further estimate that, under a “business-as-usual” climate-  
41 scenario, earlier spring arrival will enhance NPP of temperate forests by ~0.2 Gt per year at the  
42 end of the century. In contrast, previous estimates based on a simple degree-day model range  
43 around 0.8 Gt. As such, the expected NPP of temperate forests is drastically reduced in our  
44 updated model relative to previous estimates – by a total of ~25 Gt over the rest of the century.  
45 These findings reveal important environmental constraints on the productivity of broadleaf  
46 deciduous trees and highlight that shifting spring phenology is unlikely to slow the rate of  
47 warming by offsetting anthropogenic carbon emissions.

48

49 **Keywords:** Climate change, Phenology, Spring leaf-out, Carbon cycle, Terrestrial carbon sink,  
50 Temperate forests

51

52

## 53 **Introduction**

54 Shifts in the timing of annual growth cycles in temperate trees have direct impacts on global  
55 biogeochemical cycles (Keenan et al., 2014; Richardson et al., 2010), species distribution  
56 patterns (Chuine, 2010), and ultimately feedback to the climate system by affecting the  
57 atmospheric carbon budget (Richardson et al., 2013). There is broad consensus that warming  
58 trends over the past decades have led to an earlier arrival of spring leaf emergence in Northern  
59 Hemisphere temperate trees, a trend that is enhancing global primary productivity under climate  
60 change (Keenan et al., 2014; Menzel & Fabian, 1999; Zohner & Renner, 2014). Depending on  
61 species and location, leaf emergence has advanced by 3–8 days for every degree increase in air  
62 temperature (Cook et al., 2012; Menzel & Fabian, 1999; Zohner & Renner, 2014). However, a  
63 growing body of evidence suggests that this past trend cannot be used to predict future  
64 responses, because other environmental factors may constrain the future advances in spring  
65 phenology (Laube et al., 2014; Polgar et al., 2014; Zohner et al., 2016, 2017). Aside from spring  
66 temperature, most temperate trees rely on additional factors, including winter chilling and day-  
67 length, that are likely to become limiting in the future (Laube et al., 2014; Polgar et al., 2014;  
68 Zohner et al., 2016, 2017). Yet, a lack of information about the existence, or relative importance  
69 of these drivers translates to high uncertainty in model predictions of future forest phenology  
70 (Basler, 2016). Given that each day advance in spring leaf unfolding of deciduous trees  
71 translates to an increase in net ecosystem carbon uptake of 4.5 gC m<sup>-2</sup> (Keenan et al., 2014),  
72 untangling these mechanisms is critical for improving confidence in future climate projections.

73 Three main factors — autumn temperatures (Fu et al., 2014; Heide, 2003), winter  
74 chilling (Laube et al., 2014; Luedeling et al., 2011; Yu et al., 2010; Zohner et al., 2017), and  
75 day length (Heide, 1993b, 1993a; Körner & Basler, 2010) — have been proposed to control  
76 spring leaf-out by modulating the amount of warming that trees require to leaf-out. These  
77 factors serve trees as a safety mechanism to prevent precocious leaf-out in case of an early  
78 warm spell when the risk of nightly freezing is still high (Körner & Basler, 2010; Zohner, Mo,

79 Renner, et al., 2020; Zohner, Mo, Sebald, et al., 2020). Each of these factors is therefore likely  
80 to counteract the advances in spring onset under a warming climate. Specifically, as the climate  
81 warms, the accumulated warming required for leaves to emerge is expected to increase because:  
82 (i) warmer autumn temperatures delay the initiation of dormancy (Fu et al., 2014; Heide, 2003);  
83 (ii) warmer winters lead to reduced chilling accumulation (Fu et al., 2015; Zohner & Renner,  
84 2014); and (iii) days at spring onset are becoming shorter (Fu et al., 2019a; Heide, 1993b;  
85 Vitasse & Basler, 2013; Zohner & Renner, 2015) (Fig. 1).

86         The potential effects of these separate environmental drivers have been identified  
87 using controlled climate chamber experiments with pot plants or twig cuttings (Laube et al.,  
88 2014; Polgar et al., 2014; Zohner et al., 2016). These studies provide valuable mechanistic  
89 insights, but they do not necessarily reflect the behavior of mature trees under natural growing  
90 conditions (Vitasse, 2013). Although the inclusion of these hypothesized mechanisms can  
91 improve the performance of mechanistic phenological models, the exact nature, and relative  
92 importance, of these mechanisms remains untested under natural conditions (Fu et al., 2019a).  
93 As such, we cannot represent these mechanisms in global biogeochemical models to predict the  
94 consequences for future temperate forest productivity. Parameterizing phenological models and  
95 translating their effects into global biogeochemical models requires direct empirical evidence  
96 about the effects of these dominant environmental drivers in mature trees exposed to real-world  
97 changes in natural environmental conditions (Chen et al., 2016).

98         To represent the important phenological mechanisms into larger biogeochemical  
99 models, we need unifying evidence for the strength and direction of these ecological  
100 parameters. Empirically testing the influence of these environmental constraints is also vital for  
101 avoiding overparameterization in global biogeochemical models, which need to rely on simple  
102 sub-models to represent plant physiological processes. To date, dynamic global vegetation  
103 models, such as LPJ-GUESS, cannot reflect the complex dynamics that are represented in  
104 specialized phenology models. As such, they can only account for spring phenology using a

105 simple degree-day–chilling relationship, neglecting the important physiological mechanisms  
106 that are likely to restrict the advance of spring phenology in the future. These models are thus  
107 likely to vastly overestimate the advances in spring phenology over the rest of the century.  
108 Addressing this huge source of uncertainty necessitates that we generate simple empirical  
109 parameters for the combined roles of autumn temperature, winter chilling and day length.

110         In this study, we aim to bridge the gap between specialized phenological models and  
111 global vegetation models by developing a simple, empirical model to evaluate the key  
112 mechanisms represented in process-based models. Using a massive *in situ* database of forest  
113 leaf-out observations, we determine the interactive effects of autumn temperature, winter  
114 chilling and spring day-length variation on thermal requirements to leaf-out in mature temperate  
115 forest trees. We then use the observed relationships to train statistical predictions of future  
116 spring arrival. By comparing this empirical model performance with all available process-based  
117 models from the phenological literature, we show that it adequately reflects the dominant  
118 drivers of spring phenology, and predicts spring leaf-out with as much accuracy as existing  
119 mechanistic models. In addition, we use forecasts of future temperatures to project the future  
120 changes in spring phenology under two climate change scenarios (“CO<sub>2</sub> stabilization” scenario,  
121 RCP 4.5 and “business-as-usual”, RCP 8.5). With high confidence in our ‘simple’ empirical  
122 model performance, we could then use the calculated coefficients to train a global dynamic  
123 vegetation model to more accurately reflect the future changes in spring phenology. Ultimately,  
124 this big-data approach enables us to test the effects of interacting climate drivers, benchmark  
125 model projections, and evaluate how these mechanisms influence global dynamic vegetation  
126 model predictions of future phenology and global net primary productivity (NPP).

127

128

129

130

## 131 **Methods**

132 **Data set.** *In situ* observations of leaf-out date were obtained from the Pan European Phenology  
133 network (Templ et al., 2018), which provides open-access phenological data for Europe (mainly  
134 Germany, Switzerland, and Austria). We selected leaf-out records of 9 common temperate tree  
135 species (7 deciduous angiosperms, 1 deciduous conifer, 1 evergreen conifer) at 4,165 sites (see  
136 Fig. S1 for site locations). For the seven angiosperms, leaf-out was defined as the date when  
137 unfolded leaves, pushed out all the way to the petiole, were visible on the respective individual  
138 (BBCH 11, Biologische Bundesanstalt, Bundessortenamt und Chemische Industrie). For the  
139 two conifers *Larix decidua* and *Picea abies* leaf-out was defined as the date when the first  
140 needles started to separate (“mouse-ear stage”; BBCH 10).

141 Information on temperature parameters was derived from a gridded climatic data set  
142 of daily minimum and maximum temperatures at 0.5° spatial resolution (approximately 50 km)  
143 (Beer et al., 2014). We additionally tested the CRU/NCAR dataset  
144 (<https://crudata.uea.ac.uk/cru/data/ncep/>) which also contains daily minimum and maximum  
145 temperatures at 0.5° spatial resolution and obtained very similar results ( $R^2$  for degree-days  
146 extracted from ref (Beer et al., 2014) vs. CRU/NCAR dataset = 0.94). Future predictions of  
147 daily maximum and minimum temperatures were based on two different climate warming  
148 scenarios (RCP 4.5 and 8.5) (Beer et al., 2014).

149 **Data cleaning.** Following (Vitasse et al., 2017), we removed (i) leaf-out dates that deviated  
150 from an individual’s median more than 3 times the median absolute deviation (moderately  
151 conservative threshold), (ii) leaf-out dates for which the accumulated degree-days deviated  
152 from an individual’s median degree-days more than 3 times the median absolute deviation, and  
153 (iii) individuals, for which the standard deviation of phenological observations across years was  
154 higher than 15. This data cleaning removed 10% of the data, resulting in a total of 24,650 time-  
155 series and 727,401 phenological observations (individuals x years), with a median time-series  
156 length of 29 years (minimally 15 years, maximally 63 years).

157 **Environmental parameters.** Accumulated warming to leaf-out was calculated as the growing  
 158 degree-days (using 5°C as base temperature) from 1 January until the date of leaf unfolding.  
 159 We also tested a temperature threshold of 0 °C, which produced very similar results. Here, we  
 160 only report the results using the threshold of 5 °C. To calculate degree-days, we approximated  
 161 hourly temperature values with a sine curve based on daily maximum ( $T_{max}$ ) and minimum  
 162 temperatures ( $T_{min}$ ) [equation 1], subtracted 5 (base temperature) from each value, then set all  
 163 values below the base temperature to zero (because negative development is biologically not  
 164 possible), and finally calculated the mean of all 24 values for each day, weighting day-time  
 165 values (= time when sun is above the horizon) 3 times more than night-time values. This  
 166 weighting was done because the effect of day-time temperature on leaf unfolding is ~3 times  
 167 higher than that of night-time temperature (Fu et al., 2016; Piao et al., 2015).

168 Winter chilling, reflecting the sum of chilling from 1 October until the mean leaf-out  
 169 date of each individual, was calculated in two ways (either temperatures below 5 °C, or between  
 170 0 – 5 °C) to reflect two possibilities proposed in the literature (Coville, 1920; Fu et al., 2015;  
 171 Hunter & Lechowicz, 1992). Temperature ( $T_{hour}$ ) at any time of the day ( $time_{day}$ ) was simulated  
 172 with a sine curve based on daily maximum ( $T_{max}$ ) and minimum temperatures ( $T_{min}$ ) using the  
 173 following equation:

174

$$175 \quad T_{hour} = \frac{(T_{max} - T_{min})}{2} * \sin\left(\frac{\pi}{12} * time_{day} - \frac{\pi}{2}\right) + \frac{(T_{max} + T_{min})}{2} \quad (1)$$

176

177 This allowed us to calculate the daily proportion of chilling, rather than using a simple  
 178 presence/absence classification based on daily mean temperatures (e.g., (Fu et al., 2015)).  
 179 Multiple studies have reported that temperatures slightly above freezing are most effective in  
 180 satisfying chilling requirements and assume that effective chilling temperatures range between  
 181 0 °C and 5 °C (Coville, 1920; Vitasse et al., 2017):

182



$$183 \quad \text{Chill}_{hour} = 1 \quad \text{if } 0 \leq T \leq 5 \quad (2)$$

184

185 where chilling ( $\text{Chill}_{hour}$ ) at any given time of the day depends on the temperature ( $T$ ).

186 We then calculated daily chilling proportions, e.g., a day in which in 75% of the time  
187 temperatures are between 0°C and 5 °C translates to 0.75 chilling days.

188 In addition, we calculated winter chilling including all temperatures below or equal to

189 5 °C (Fu et al., 2015) as:

190

$$191 \quad \text{Chill}_{hour} = 1 \quad \text{if } T \leq 5 \quad (3)$$

192

193 To calculate the timing of spring onset for each year, we first needed to define a date reflecting

194 the onset of spring warming. To do so, for each site and species combination, we calculated the

195 average degree-days accumulating before leaf-out. Spring onset (SO) each year was then

196 defined as the day length at the date when the average degree-days to leaf-out at the respective

197 site were reached (Forsythe et al., 1995). SO thus reflects how early spring warming occurred

198 each year.

199

$$200 \quad \text{SO} = 24 - \frac{24}{\pi} \cos^{-1} \left[ \frac{\sin \frac{0.8333\pi}{180} + \sin \frac{L\pi}{180} \sin \varphi}{\cos \frac{L\pi}{180} * \cos \varphi} \right] \quad (4)$$

201

$$202 \quad \varphi = \sin^{-1} (0.29795 * \cos \theta) \quad (5)$$

203

$$204 \quad \theta = 0.2163108 + 2 * \tan^{-1} (0.9671396 * \tan (0.00860 * (\text{DOY} - 186))) \quad (6)$$

205

206 where  $L$  is the latitude of the phenological site and DOY is the day of year when the average

207 degree-days to leaf-out at each site were reached.

208 To infer information on autumn temperatures in the year preceding leaf unfolding, we  
209 calculated the mean temperatures of the months September and October, September–  
210 November, or October and November for each year.

211 For each species and site, we also analysed the relationship between spring  
212 temperatures and leaf-out dates (Fig. S9). Spring temperature for each year and individual was  
213 defined as the average temperature during the 60 days prior to the average leaf-out date of an  
214 individual.

215

216 **Analysis.** To test for the importance of autumn temperatures, winter chilling, and spring day-  
217 length on warming required to leaf-out at each site, we applied univariate regression models  
218 over time at the individual-level (Fig. 2). To visualize the correlations for each species, we  
219 removed noise that is due to between-site variation using mixed effects models (R-package  
220 lme4) [Fig. S2]. We calculated chilling in two ways (equations 2 and 3), and, in all nine species,  
221 the effect of chilling on the amount of warming required to leaf-out was significantly higher  
222 when choosing the second option (all temperatures  $\leq 5^{\circ}\text{C}$  satisfy chilling requirements; Fig.  
223 2b). To remove possible covariate effects of day-length, we also applied partial correlation  
224 analyses between winter chilling and spring warming and obtained similar results, i.e., in all  
225 nine species, partial correlation coefficients were higher when using all temperatures  $\leq 5^{\circ}\text{C}$  to  
226 calculate winter chilling. Similarly, we tested which temperature period in autumn best predicts  
227 the amount of warming required to leaf-out, and for each time-series, the autumn temperature  
228 period that yielded the highest correlation coefficient was chosen for multivariate modelling.

229 We used breakpoint analysis (Richardson et al., 2018), based on the residual sums of  
230 squares, to test whether the effect of the timing of spring onset or winter chilling on required  
231 accumulated warming is linear or whether the observed response is flattening beyond a  
232 threshold. In 70% and 76% of all time-series, a linear model was preferred over a breakpoint  
233 model for the effect of the timing of spring onset or winter chilling, respectively, on required

234 accumulated warming. For the 30% and 25% of time series in which a breakpoint was inferred,  
235 we investigated whether steeper slopes are preferred with an earlier arrival of spring warming  
236 or decreasing chilling. For the timing of spring onset, a steeper slope at earlier dates was  
237 preferred for only 15% of pixels, while the opposite pattern also was preferred for 15% of  
238 pixels. For chilling, a steeper slope under low chilling was only inferred for 13% of pixels,  
239 while the opposite pattern was inferred for 11%. We thus rejected the hypothesis that the effect  
240 of the timing of spring onset or winter chilling on the amount of warming required to leaf-out  
241 is non-linear, i.e., increases with earlier arrival of spring warming or decreasing chilling.

242         After we had chosen the best autumn period and chilling model for each species, we  
243 modelled individual warming requirements using multivariate linear models. Sixteen models  
244 were tested against each other (Fig. S3a). The models always included winter chilling and day-  
245 length as fixed effects. Additionally, we either included or excluded autumn temperatures as  
246 explanatory variable. We also tested for an interaction term between day-length and winter  
247 chilling, because day-length and chilling cues can interact, with long days substituting for  
248 insufficient chilling and *vice versa* (Vitasse & Basler, 2013; Zohner & Renner, 2015). We also  
249 tested models including chilling and the timing of spring onset as exponential terms (which did  
250 not affect model precision and projections; Figs. S5 and S6). In addition to our multivariate  
251 model (hereafter referred to as *full model*), we applied a *chilling model* (which has previously  
252 been implemented in the LPJ-GUESS dynamic global vegetation model), in which the amount  
253 of warming required to leaf-out is solely affected by winter chilling (equation 7), and a *null*  
254 *model*, in which leaf-out is solely driven by spring warming (degree-day accumulation) to test  
255 for the importance of these individual mechanisms.

256         By contrast to more complex phenological models, the starting date of degree-day  
257 accumulation was not fitted to the observed data and instead fixed to the first day of the year,  
258 allowing for easy incorporation into large-scale vegetation models. This also ensures that the  
259 *null model* (warming-only model) is not confounded by other factors because fitting a starting

260 date of degree-day accumulation implicitly accounts for winter chilling and/or day-length by  
261 determining when plants become susceptible to spring warming.

262 All models were fitted separately to individuals, because we were interested in  
263 temporal patterns within individuals (rather than spatial patterns among individuals), and spring  
264 warming, day-length, and chilling requirements differ among individuals (Zohner et al., 2018).  
265

### 266 *Process-based phenological models*

267 We ran 17 parameterized process-based phenological models from the literature to test the  
268 overall performance of our *full model* against existing models. We used the R-package  
269 PHENOR (Hufkens et al., 2018) to calibrate the models. Model parameters were optimized  
270 using the GenSA algorithm (Xiang et al., 2013), combining both the Boltzmann machine and  
271 faster Cauchy machine simulated annealing approaches for fast optimizations (Tsallis &  
272 Stariolo, 1996). According to (Hufkens et al., 2018), the number of iterations was set to 40,000  
273 with a starting temperature of 10,000.

274

### 275 *Model evaluation*

276 To judge the performance of phenological models, previous studies relied either solely on root-  
277 mean square errors (RMSEs) of observed vs predicted leaf-out dates (Basler, 2016; Fu et al.,  
278 2012; Vitasse et al., 2018) or additionally evaluated model predictions by comparing predicted  
279 (in the y-axis) vs observed (in the x-axis) leaf-out dates (Delpierre et al., 2009; Hufkens et al.,  
280 2018; Schaber & Badeck, 2003). However, such regression to evaluate models is incorrect,  
281 leading to erroneous estimates of the slope and intercept (Piñeiro et al., 2008). Especially in  
282 directional models such as spring phenological projections, where future climate conditions  
283 will lead to ever earlier occurrence dates, models need to be evaluated by analyzing intercept  
284 and slope components of observed (in the y-axis) vs predicted dates (in the x-axis). To do so,  
285 we conducted Wald-test based comparisons (Fox, 2016) using the linearHypothesis function in

286 the R-package car, allowing us to test for each individual site whether the slopes and intercepts  
287 of observed *vs.* predicted leaf-out dates differ significantly from 1 and 0, respectively (Fig.  
288 4a,b). For each species, we also obtained the overall model fit ( $R^2$  values) and RMSEs for  
289 observed *versus* predicted values (Figs. 3c, 4c, and S4). Next, we applied 10-fold cross-  
290 validations (M. Stone, 1974), and tested whether projected leaf-out dates capture (i) observed  
291 temporal trends and (ii) the observed sensitivity of leaf-out dates to spring temperatures (Figs.  
292 3a,b, S5, and S6). To calculate temperature sensitivity trends based on time-series, we had to  
293 remove noise that is due to between-site variation. This was done by adjusting the data using  
294 mixed effects modelling available through the R-package lme4.

295

#### 296 *Future projections of spring onset*

297 To examine how the analysed ecological mechanisms influence future projections of spring  
298 leaf-out, we extrapolated the timing of spring leaf-out until 2100 using two future climate  
299 scenarios (“CO<sub>2</sub> stabilization” scenario, RCP 4.5 and “business-as-usual”, RCP 8.5; Fig. S7).  
300 Specifically, for each scenario, we ran statistical extrapolations of future leaf-out dates, based  
301 on the seven best-performing phenology models, including our *full model*, and the simple *null*  
302 *model* accounting solely for temperature accumulation. Future projections of daily minimum  
303 and maximum temperatures came from (Beer et al., 2014) (Fig. S7). Emissions in the RCP 4.5  
304 climate scenario peak around 2040 and then decline. In the RCP 8.5 climate scenario emissions  
305 continue to rise throughout the 21<sup>st</sup> century.

306

#### 307 *Land-surface flux projections*

308 We used LPJ-GUESS, a dynamic global vegetation model (Smith et al., 2014), to simulate the  
309 effects of shifting spring phenology on temperate forest net primary productivity (NPP). LPJ-  
310 GUESS represents vegetation growth and dynamics using a mixture of plant functional types  
311 that respond to forcing from the climate (temperature, precipitation, incoming shortwave

312 radiation), atmospheric CO<sub>2</sub> mixing ratios and soil type. The successional structure of  
313 vegetation is simulated using multiple (here ten) replicate patches in each grid cell, which are  
314 subject to stochastic processes of establishment and mortality. Photosynthesis, respiration,  
315 stomatal conductance and phenology in LPJ-GUESS are simulated on a daily time step.

316         Limitations in availability of the necessary driving data and requirements for  
317 parsimony to operate at large-scales mean that common process-based phenological models  
318 cannot easily be incorporated into global vegetation models such as LPJ-GUESS. Instead, in  
319 common with most other such models (Clark et al., 2011; Krinner et al., 2005), spring  
320 phenology was represented by an exponential relationship between growing degree-days to  
321 leaf-out and the length of the chilling period (*chilling model*). In LPJ-GUESS the relationship  
322 was formulated as follows (Sykes et al., 1996):

323

$$324 \quad \text{GDD}^\circ = \alpha + \beta e^{-\kappa C} \quad (7)$$

325

326 where C is the length of the chilling period and  $\alpha$ ,  $\beta$ , and  $\kappa$  are constants specific to plant  
327 functional types.

328

329 Based on our empirical findings we replaced this equation by the following (*full model*):

330

$$331 \quad \text{GDD}^\circ = \alpha + \beta C + \gamma D + \delta CD \quad (8)$$

332

333 where C is the length of the chilling period, D is the timing of spring warming, CD is the  
334 interaction between chilling and the timing of spring warming, and  $\alpha$ ,  $\beta$ ,  $\gamma$ , and  $\delta$  are coefficients  
335 specific to plant functional types (table S1). The length of the chilling period was defined as  
336 the number of days  $<5^\circ\text{C}$  from 1 October, the timing of spring warming was defined relative to  
337 a degree-day threshold (table S1). We calculated a specific spring onset for each functional type

338 because, the needleleaf summergreen species *Larix decidua*, for example, flushes earlier than  
339 many broadleaf summergreen trees. Three functional types of trees (BSI, broadleaved  
340 summergreen shade-intolerant; BST, broadleaved summergreen shade-tolerant; NS,  
341 needleleaved summergreen) were present in our species sampling. Following (Niinemets &  
342 Valladares, 2006), *Fagus sylvatica* and *Tilia cordata* were treated as shade tolerant, *Aesculus*  
343 *hippocastanum*, *Alnus glutinosa*, *Betula pendula*, *Fraxinus excelsior*, and *Quercus robur* as  
344 shade intolerant. Leaf-out phenology of *Picea abies* was not included in LPJ-GUESS because,  
345 in evergreen species, onset of photosynthetic activity in spring is not dependent on the flushing  
346 of new buds. In addition to the deciduous plant functional types described above, LPJ-GUESS  
347 simulations also included a temperate needleleaved evergreen tree, a boreal needleleaved  
348 evergreen shade-tolerant tree, a boreal needleleaved evergreen shade-intolerant tree and a C3  
349 grass (Smith et al., 2014), with the distributions of each functional type governed by model-  
350 internal processes of competition. All simulations were run as potential natural vegetation (i.e.  
351 without land management) and the outputs were masked and rescaled to current temperate  
352 forest area as defined by (Hansen et al., 2013).

353         Daily climate forcing data came from the r1i1p1 ensemble member of the IPSL-  
354 CM5A-LR model from CMIP5 (Taylor et al., 2012) for 1850-2099 following the RCP 8.5  
355 scenario, bias-corrected to 1960-1999 WATCH climate (Hempel et al., 2013), as prepared for  
356 the ISI-MIP2 project. Atmospheric CO<sub>2</sub> mixing ratios were as prescribed for the RCP 8.5  
357 scenario of CMIP5 and N deposition data was taken from Lamarque et al. (Lamarque et al.,  
358 2013). Simulations were spun-up for 500 years using recycled, detrended 1850-1879 climate,  
359 and 1850 atmospheric CO<sub>2</sub> mixing ratio and N deposition. They were then run under fully  
360 transient environmental forcings from 1850-2099. The spatial resolution was 0.5° x 0.5°. In  
361 total four simulations were conducted: simulations with the original and updated phenology  
362 algorithms, and two further simulations in which, for each of the algorithms, leaf out dates from  
363 2010 onwards were forced by mean 2001-2010 daily temperatures in each grid cell, so as to

364 provide a baseline from which to identify the effects of the phenology algorithm on the carbon  
365 cycle.

366

## 367 **Results**

### 368 *The environmental drivers of spring leaf-out*

369 Our linear univariate models showed that, while autumn temperatures had a relatively  
370 minor effect, both winter chilling ( $P < 0.001$ ; Correlation coefficient = 0.4 – 0.5) and day-length  
371 ( $P < 0.001$ ; Correlation coefficient = 0.5 – 0.7) had consistent negative effects on accumulated  
372 warming required to leaf-out across all species (Figs. 2 and S2). When chilling was calculated  
373 using all temperatures below 5°C, the model outperformed an equivalent model in which  
374 effective chilling temperatures range between 0 and 5°C (Fig. 2b).

375 The best-performing multivariate model (lowest AIC and highest  $R^2$ ) included chilling  
376 and the timing of spring onset as fixed effects and an interaction between winter chilling and  
377 the timing of spring onset (Figs. 3 and S3a). Across all species, this *full model* adequately  
378 predicted the accumulated warming required to leaf-out across 727,401 observations over 63  
379 years (average  $R^2$  and RMSE = 0.5 and 5.5, respectively; Figs. S3a and S4a).

380 On average, across all species, observed leaf-out dates advanced by  $3.8 \pm 0.1$  days per  
381 each degree increase in air temperature. The *full model* performed well in predicting this  
382 temperature sensitivity, predicting  $3.7 \pm 0.2$  days/°C. In contrast, the *chilling* and *null model*  
383 over-estimated leaf emergence, predicting  $4.9 \pm 0.2$  and  $6.3 \pm 0.2$  days/°C, respectively (Fig.  
384 3b).

385

### 386 *Evaluating phenology model performance*

387 Compared to all existing phenology models, our empirical model performed well in  
388 predicting leaf emergence over the last 15 years of leaf-out observations, explaining over 50%  
389 of the variation in spring leaf emergence over 727,401 observations. This was only marginally



390 worse explanatory power than the best available phenology models (see RMSE values in Fig.  
391 4c). Our *full model* also showed high model-accuracy, with predictions fitting close to the 1:1  
392 line in predicted vs. observed plots (Fig. 4c). As such, the intercept and slope components of  
393 observed vs. predicted comparisons of leaf-out dates for our *full model* were among the least  
394 likely to differ from 1 and 0, respectively, with a significant ( $P < 0.05$ ) deviation only found for  
395 <2% of sites (Fig. 4 a,b). Four of the other process-based models showed an equally low  
396 proportion of significant sites with exceptionally high model accuracy. Model accuracy was  
397 slightly lower for 11 models (2–6% significant sites), while the remaining 4 models all  
398 performed considerably worse (13–88% significant sites) [Fig. 4 a,b]. The best-performing  
399 model was the M1 model both in terms of model explanatory power and accuracy.

400

#### 401 *Future projections of spring leaf-out*

402 For both climate scenarios, the seven best models (including our *full model*) gave very  
403 similar future predictions, estimating a ~60% reduction in the phenological response rates to  
404 global warming compared to what would be expected if spring warming was the sole driver of  
405 leaf-out phenology (i.e., the *null model*) [Fig. 4d]. While the *null model* predicted 25-days  
406 earlier leaf unfolding by the end of the 21<sup>st</sup> century under a “business-as-usual” scenario, the  
407 best-performing models estimated advances of only 11 days. Our *full model* projected similar  
408 responses for all species, with the exception of *Fagus sylvatica* (Fig. S8), which is expected to  
409 advance leaf-out dates less than the other species because pronounced chilling and day length  
410 constraints (Fig. 2) cause a lower temperature sensitivity (3.0 days/°C) compared to the other  
411 study species (Figs. S6 and S9).

412

#### 413 *Changes in temperate forest productivity*

414 The standard LPJ-GUESS model (including a simple chilling–degree-day function to  
415 predict spring phenology) estimated that, under a “business-as-usual” climate-scenario, earlier

416 spring arrival will enhance NPP of temperate forests by  $\sim 0.8$  Gt carbon per year at the end of  
417 the century, resulting in a total increase of cumulative spring NPP of 37 Gt carbon over the rest  
418 of the century. In contrast, the updated model, including the new empirically-derived  
419 information about the ecological constraints on spring phenology (table S1), estimated that  
420 earlier spring arrival will enhance NPP of temperate forests by only  $\sim 0.2$  Gt per year at the end  
421 of the century, resulting in a total increase of only 12 Gt over the rest of the century (Figure 5).

422

## 423 **Discussion**

424 Our analyses show that, across all nine tested species, winter chilling and the timing of  
425 spring onset have consistent negative effects on the accumulated warming required to leaf-out  
426 (Figs. 2 and S2). In line with previous studies (Heide, 1993b; Vitasse & Basler, 2013; Zohner  
427 et al., 2016), European beech showed the strongest sensitivity to chilling and the timing of  
428 spring onset (Fig. 2b, c), but the limiting effects of both variables were consistent across all  
429 temperate tree species. As such, although spring warming is likely to increase over the rest of  
430 the century, the reductions in winter chilling and the timing of spring onset are likely to  
431 constrain the advance in spring leaf emergence over the rest of the century. These limiting  
432 mechanisms may be an important safety strategy against precocious leaf development under  
433 future spring climates that overall will be warmer but also more variable, counterintuitively  
434 increasing trees' risk of late frost damage to their young leaves in many Eurasian temperate  
435 forests (Zohner, Mo, Renner, et al., 2020). In those regions where late frost risk is strongly  
436 increasing with climate change, conservative, late-flushing species or populations with  
437 pronounced chilling and daylength requirements will be least likely to experience leaf frost  
438 damage during spring (Vitasse et al., 2018; Zohner, Mo, Sebald, et al., 2020).

439 While our findings suggest that the timing of the onset of spring warming, represents a  
440 strong control on leaf emergence across all nine studied tree species (see Fu *et al.* (2019b) for  
441 a more detailed test of this relationship), it remains unclear what is ultimately driving this

442 relationship. A possible explanation for the negative relationship between the amount of  
443 warming required to leaf-out and the ‘earliness’ of spring onset is day length. Yet, experimental  
444 studies revealed that only in a few species, such as *Fagus sylvatica*, does day length have an  
445 effect on spring leaf-out timing (Laube et al., 2014; Zohner et al., 2016). It is therefore also  
446 possible that the time effect we detect here could ultimately be driven by mechanisms other  
447 than day length, such as time *per se* (sensed through an internal clock) or changes in spectral  
448 light composition (Brelsford & Robson, 2018). Our results do not give mechanistic insights that  
449 would allow us to disentangle the mechanisms by which plants sense the time of the year, but  
450 they provide important evidence that both winter chilling and the timing of the onset of spring  
451 warming modulate the amount of warming required to leaf-out, thereby restricting future  
452 advances in leaf emergence under climate change.

453         In contrast to previous suggestions (Fu et al., 2015; Vitasse et al., 2017; Vitasse &  
454 Basler, 2013), our results suggest that below-zero temperatures are effective in fulfilling  
455 chilling requirements. The model in which chilling was calculated using all temperatures below  
456 5°C outperformed an equivalent model in which effective chilling temperatures ranged between  
457 0 and 5°C (Fig. 2b). Our results further show that autumn temperatures have a negligible effect  
458 on next year’s leaf-out dates (Fig. 2a). Yet, autumn temperatures might be of increasing  
459 importance in the future if continued autumn warming will further delay the initiation of  
460 dormancy, thereby leading to a reduction in winter chilling.

461         To predict the amount of warming required for each tree to leaf-out, we ran multivariate  
462 models, including all three factors (autumn temperature, winter chilling, and the timing of  
463 spring onset) and the interactions between them. The best model included chilling and the  
464 timing of spring onset as fixed effects, and an interaction between winter chilling and the timing  
465 of spring onset (Fig. S3a). This interaction term is supported by experimental studies showing  
466 that winter chilling can substitute for day length and *vice versa* (Heide, 1993b, 1993a; Laube et  
467 al., 2014; Zohner et al., 2016; Zohner & Renner, 2015). The coefficients in these empirical

468 models reveal parameters for each of the dominant environmental drivers of spring phenology  
469 that are necessary for predicting changes in leaf-out over time.

470 To test for the importance of these ecological mechanisms, we compared the predictions  
471 of our *full model* (including spring warming, timing of spring onset, and winter chilling) against  
472 similar empirical models that lack these mechanisms. Specifically, we compared the  
473 performance of our *full-model* to a simple “*null model*”, which included only spring warming,  
474 and a “*chilling model*” (see equation 7) – including spring warming and winter chilling – which  
475 has previously been implemented in the LPJ-GUESS dynamic global vegetation model. Our  
476 *full model* performed well in predicting the observed temperature sensitivity of  $3.8 \pm 0.1$  days  
477 per each degree increase in air temperature, predicting  $3.7 \pm 0.2$  days/°C. In contrast, because  
478 they lack the ecological mechanisms that might restrict future advances in spring leaf-out, the  
479 *chilling* and *null model* over-estimated leaf emergence, predicting temperature sensitivities of  
480  $4.9 \pm 0.2$  and  $6.3 \pm 0.2$  days/°C, respectively (Fig. 3b). The inclusion of all three mechanisms  
481 therefore vastly improved model accuracy, but more importantly, this reduced the over-  
482 estimation of spring leaf-emergence in extremely warm years (Fig. 3a). This demonstrates that  
483 the combined roles of winter chilling, the timing of spring onset, and spring warming need to  
484 be accounted for in predictions of future tree phenology and productivity.

485 We also compared the performance of our full model against 17 process models from  
486 the literature to evaluate whether our full empirical model is capturing the mechanisms in  
487 existing state-of-the-art phenology models (Fig. 4). We stress that, even though some of these  
488 models are called “*ecodormancy models*” (suggesting that they solely consider spring warming  
489 as a factor), all of these models at least implicitly account for winter chilling- / day length-  
490 induced endodormancy release by fitting specific starting dates of degree-day accumulation to  
491 the data (we therefore refer to them as explicit or implicit endodormancy models hereafter).  
492 Although fitting a specific starting date of degree-day accumulation cannot reflect the gradual  
493 transition from endo- to ecodormancy (see e.g., Fig. 2 in Zohner & Renner (2015)), these

494 models all directly or indirectly represent the ecological mechanisms that we have evaluated in  
495 our *full model*.

496 By accurately representing the three dominant factors regulating spring leaf-out, our  
497 simple empirical model performed as well as the best-performing phenology models. In doing  
498 so, our statistical approach can provide a benchmark, revealing which mechanistic models are  
499 most accurately representing the eco-physiological mechanisms regulating spring leaf-out.  
500 Compared to all existing phenology models, our empirical model had only marginally worse  
501 explanatory power than the best available phenology models (Fig. 4c) and excelled in terms of  
502 model-accuracy (intercept and slope components of observed vs. predicted leaf-out dates; Fig.  
503 4 a,b). Four of the other process-based models showed an equally high model accuracy, with  
504 the M1 model performing best. This high predictive accuracy of the top 4 process-based models  
505 is in direct contrast with previous studies, which suggested low performance across all  
506 phenology models (Basler, 2016). This distinction is likely to arise from our focus on model  
507 accuracy (i.e. slope estimates) rather than model fit (i.e. root mean squared error), and the test  
508 if predicted values (in the x-axis) reflect observations (in the y-axis), not *vice versa* (Piñeiro et  
509 al., 2008) (see Methods).

510 Our simple empirical model was trained on current climate conditions, which can lead  
511 to uncertainties in future projections if environmental conditions fall outside the model training  
512 range. Yet, as expected from the high predictive accuracy of the top models, the seven best  
513 models gave very similar future predictions, with our *full model* and the best-performing M1  
514 model representing the same leaf-out trajectories (Fig. 4d). Compared to our *null model*, in  
515 which spring warming was the sole driver of leaf-out phenology, the top models estimated a  
516 ~60% or 14 days reduction in the phenological responses to global warming (Fig. 4d). This  
517 demonstrates that, despite different parameters and assumptions, there is a broad consensus  
518 among phenology models – including our *full model*. As such, our simple regression model  
519 can serve to provide basic parameters that can easily be incorporated into large-scale vegetation

520 models and Earth system models to project future terrestrial vegetation carbon dynamics. More  
521 complex phenological models rely on spatially-explicit parameter-optimization algorithms to  
522 account for endodormancy release. Capturing the spatial variation across temperate forests  
523 would require large amounts of spatially-uniform phenological data to train these models. Such  
524 data does not currently exist and would require a huge coordinated sampling effort. In contrast,  
525 our regression model offers a highly parsimonious approach, reflecting the main mechanisms  
526 triggering spring phenology without the limitations of model overparameterization. This  
527 approach can therefore provide projections of increased veracity without inflating structural  
528 uncertainty, which remains the main cause of divergence in vegetation model projections  
529 (Nishina et al., 2015). Our model can thus provide the empirical relationships that are needed  
530 to underpin future projections of temperate spring phenology, and its impacts on terrestrial  
531 vegetation carbon dynamics.

532         To finally comprehend how our leaf-out predictions will affect future projections of  
533 NPP, we used a dynamic global vegetation model (LPJ-GUESS). Previously, spring phenology  
534 was implemented as a function of degree-days and winter chilling (see *chilling model* in Figs.  
535 3, 4, and 5) (Sykes et al., 1996). We parameterized the phenology algorithm using the  
536 empirically-derived relationships with the timing of spring onset, and the updated estimates of  
537 winter chilling (table S1). These changes drastically reduced the projected increases in  
538 temperate forest productivity over the rest of this century. Specifically, the standard LPJ-  
539 GUESS model (including chilling-only) estimates that cumulative temperate forest NPP will  
540 increase over the rest of the century by a total of 37 Gt carbon as a result of earlier spring onset.  
541 However, the updated model, including the new empirically-derived information about the  
542 ecological constraints on spring phenology estimates an increase of only 12 Gt over the same  
543 time period (Figure 5). These differences highlight the need for an improved representation of  
544 plant phenology when predicting vegetation dynamics and the terrestrial carbon cycle. The high  
545 predictive accuracy of state-of-the-art phenology models we detect here demonstrates that it is

546 possible to adequately represent the main environmental drivers of phenology and future efforts  
547 should thus be directed toward integrating these relevant drivers within boreal, temperate, and  
548 tropical ecosystems in global vegetation models.

549

## 550 **Conclusions**

551 Our big data approach enables us to test the effects of the three main ecological factors –winter  
552 chilling, day-length, and spring warming – that regulate the timing of spring leaf emergence in  
553 temperate forest trees. A simple statistical model reflecting these interactive ecological drivers  
554 performed as well as the best existing phenology models at predicting spring leaf-out over  
555 24,650 individual time series, highlighting that these mechanisms are critical for representing  
556 future changes in spring leaf-out. Although spring warming is likely to increase over the rest of  
557 the century, the reductions in winter chilling and an earlier timing of spring warming are likely  
558 to constrain the future advances in spring leaf emergence. Our statistical model reveals unifying  
559 parameters that can be used to represent these important phenological mechanisms in larger  
560 biogeochemical models. By representing this information into a global dynamic vegetation  
561 model, we find that the expected increases in temperate forest NPP over the rest of the century  
562 are substantially reduced relative to previous expectations, which could lead to a reduction in  
563 NPP of 0.6 Gigatons carbon per year at the end of the 21<sup>st</sup> century. These results have direct  
564 implications for future climate projections, highlighting that forest productivity will be  
565 increasingly constrained by factors aside from air temperature in the future.

566

## 567 **Data deposition statement**

568 All data used for this study is freely available through the Pan European Phenology project  
569 ([www.PEP725.eu](http://www.PEP725.eu)).

570

571

572 **References**

- 573 Basler, D. (2016). Evaluating phenological models for the prediction of leaf-out dates in six  
574 temperate tree species across central Europe. *Agricultural and Forest Meteorology*, 217,  
575 10–21. <https://doi.org/10.1016/j.agrformet.2015.11.007>
- 576 Beer, C., Weber, U., Tomelleri, E., Carvalhais, N., Mahecha, M., & Reichstein, M. (2014).  
577 Harmonized European Long-Term Climate Data for Assessing the Effect of Changing  
578 Temporal Variability on Land–Atmosphere CO<sub>2</sub> Fluxes\*. *Journal of Climate*, 27(13),  
579 4815–4834. <https://doi.org/10.1175/JCLI-D-13-00543.1>
- 580 Brelsford, C. C., & Robson, T. M. (2018). Blue light advances bud burst in branches of three  
581 deciduous tree species under short-day conditions. *Trees - Structure and Function*, 1–8.  
582 <https://doi.org/10.1007/s00468-018-1684-1>
- 583 Chen, M., Melaas, E. K., Gray, J. M., Friedl, M. A., & Richardson, A. D. (2016). A new  
584 seasonal-deciduous spring phenology submodel in the Community Land Model 4.5:  
585 impacts on carbon and water cycling under future climate scenarios. *Global Change*  
586 *Biology*, 22(11), 3675–3688. <https://doi.org/10.1111/gcb.13326>
- 587 Chuine, I. (2010). Why does phenology drive species distribution? *Philosophical*  
588 *Transactions of the Royal Society B: Biological Sciences*, 365(1555), 3149–3160.  
589 <https://doi.org/10.1098/rstb.2010.0142>
- 590 Clark, D. B., Mercado, L. M., Sitch, S., Jones, C. D., Gedney, N., Best, M. J., Pryor, M.,  
591 Rooney, G. G., Essery, R. L. H., Blyth, E., Boucher, O., Harding, R. J., Huntingford, C.,  
592 & Cox, P. M. (2011). The Joint UK Land Environment Simulator (JULES), model  
593 description – Part 2: Carbon fluxes and vegetation dynamics. *Geoscientific Model*  
594 *Development*, 4(3), 701–722. <https://doi.org/10.5194/gmd-4-701-2011>
- 595 Cook, B. I., Wolkovich, E. M., Davies, T. J., Ault, T. R., Betancourt, J. L., Allen, J. M.,  
596 Bolmgren, K., Cleland, E. E., Crimmins, T. M., Kraft, N. J. B., Lancaster, L. T., Mazer,  
597 S. J., McCabe, G. J., McGill, B. J., Parmesan, C., Pau, S., Regetz, J., Salamin, N.,



- 598 Schwartz, M. D., & Travers, S. E. (2012). Sensitivity of Spring Phenology to Warming  
599 Across Temporal and Spatial Climate Gradients in Two Independent Databases.  
600 *Ecosystems*, 15(8), 1283–1294. <https://doi.org/10.1007/s10021-012-9584-5>
- 601 Coville, F. V. (1920). The influence of cold in stimulating the growth of plants. *Proceedings*  
602 *of the National Academy of Sciences*, 6(2), 151–160. [https://doi.org/10.1175/1520-0493\(1920\)48<643b:TIOCIS>2.0.CO;2](https://doi.org/10.1175/1520-0493(1920)48<643b:TIOCIS>2.0.CO;2)
- 604 Delpierre, N., Dufrêne, E., Soudani, K., Ulrich, E., Cecchini, S., Boé, J., & François, C.  
605 (2009). Modelling interannual and spatial variability of leaf senescence for three  
606 deciduous tree species in France. *Agricultural and Forest Meteorology*, 149(6–7), 938–  
607 948. <https://doi.org/10.1016/j.agrformet.2008.11.014>
- 608 Forsythe, W. C., Rykiel, E. J., Stahl, R. S., Wu, H. i., & Schoolfield, R. M. (1995). A model  
609 comparison for daylength as a function of latitude and day of year. *Ecological*  
610 *Modelling*, 80(1), 87–95. [https://doi.org/10.1016/0304-3800\(94\)00034-F](https://doi.org/10.1016/0304-3800(94)00034-F)
- 611 Fox, J. (2016). *Applied Regression Analysis and Generalized Linear Models*. SAGE  
612 Publications, Inc.
- 613 Fu, Y. H., Campioli, M., Van Oijen, M., Deckmyn, G., & Janssens, I. A. (2012). Bayesian  
614 comparison of six different temperature-based budburst models for four temperate tree  
615 species. *Ecological Modelling*, 230, 92–100.  
616 <https://doi.org/10.1016/j.ecolmodel.2012.01.010>
- 617 Fu, Y. H., Campioli, M., Vitasse, Y., De Boeck, H. J., Van den Berge, J., AbdElgawad, H.,  
618 Asard, H., Piao, S., Deckmyn, G., & Janssens, I. A. (2014). Variation in leaf flushing  
619 date influences autumnal senescence and next year's flushing date in two temperate tree  
620 species. *Proceedings of the National Academy of Sciences*, 111(20), 7355–7360.  
621 <https://doi.org/10.1073/pnas.1321727111>
- 622 Fu, Y. H., Liu, Y., De Boeck, H. J., Menzel, A., Nijs, I., Peaucelle, M., Peñuelas, J., Piao, S.,  
623 & Janssens, I. A. (2016). Three times greater weight of daytime than of night-time

- 624 temperature on leaf unfolding phenology in temperate trees. *New Phytologist*, 212(3),  
625 590–597. <https://doi.org/10.1111/nph.14073>
- 626 Fu, Y. H., Zhang, X., Piao, S., Hao, F., Geng, X., Vitasse, Y., Zohner, C., Peñuelas, J., &  
627 Janssens, I. A. (2019a). Daylength helps temperate deciduous trees to leaf-out at the  
628 optimal time. *Global Change Biology*, 25(7), 2410–2418.  
629 <https://doi.org/10.1111/gcb.14633>
- 630 Fu, Y. H., Zhang, X., Piao, S., Hao, F., Geng, X., Vitasse, Y., Zohner, C., Peñuelas, J., &  
631 Janssens, I. A. (2019b). Daylength helps temperate deciduous trees to leaf-out at the  
632 optimal time. *Global Change Biology*, gcb.14633. <https://doi.org/10.1111/gcb.14633>
- 633 Fu, Y. H., Zhao, H., Piao, S., Peaucelle, M., Peng, S., Zhou, G., Ciais, P., Huang, M., Menzel,  
634 A., Peñuelas, J., Song, Y., Vitasse, Y., Zeng, Z., & Janssens, I. A. (2015). Declining  
635 global warming effects on the phenology of spring leaf unfolding. *Nature*, 526, 104.  
636 <http://dx.doi.org/10.1038/nature15402>
- 637 Hansen, M. C., Potapov, P. V, Moore, R., Hancher, M., Turubanova, S. a, Tyukavina, A.,  
638 Thau, D., Stehman, S. V, Goetz, S. J., Loveland, T. R., Kommareddy, A., Egorov, A.,  
639 Chini, L., Justice, C. O., & Townshend, J. R. G. (2013). High-Resolution Global Maps  
640 of 21st-Century Forest Cover Change. *Science*, 850(November), 2011–2014.  
641 <https://doi.org/10.1126/science.1244693>
- 642 Heide, O. M. (1993a). Daylength and thermal time response of budburst during dormancy  
643 release in some northern deciduous trees. *Physiologia Plantarum*, 88(4), 531–540.
- 644 Heide, O. M. (1993b). Dormancy release in beech buds (*Fagus sylvatica*) requires both  
645 chilling and long days. *Physiologia Plantarum*, 89(1), 187–191.  
646 <https://doi.org/10.1111/j.1399-3054.1993.tb01804.x>
- 647 Heide, O. M. (2003). High autumn temperature delays spring bud burst in boreal trees,  
648 counterbalancing the effect of climatic warming. *Tree Physiology*, 23(13), 931–936.  
649 <https://doi.org/10.1093/treephys/23.13.931>

- 650 Hempel, S., Frieler, K., Warszawski, L., Schewe, J., & Piontek, F. (2013). A trend-preserving  
651 bias correction – The ISI-MIP approach. *Earth System Dynamics*, 4(2), 219–236.  
652 <https://doi.org/10.5194/esd-4-219-2013>
- 653 Hufkens, K., Basler, D., Milliman, T., Melaas, E. K., & Richardson, A. D. (2018). An  
654 integrated phenology modelling framework in r. *Methods in Ecology and Evolution*,  
655 9(5), 1276–1285. <https://doi.org/10.1111/2041-210X.12970>
- 656 Hunter, A. F., & Lechowicz, M. J. (1992). Predicting the timing of budburst in temperate  
657 trees. *Journal of Applied Ecology*, 29, 597–604.
- 658 Keenan, T. F., Gray, J., Friedl, M. A., Toomey, M., Bohrer, G., Hollinger, D. Y., Munger, J.  
659 W., O’Keefe, J., Schmid, H. P., Wing, I. S., Yang, B., & Richardson, A. D. (2014). Net  
660 carbon uptake has increased through warming-induced changes in temperate forest  
661 phenology. *Nature Climate Change*, 4(7), 598–604.  
662 <https://doi.org/10.1038/nclimate2253>
- 663 Körner, C., & Basler, D. (2010). Phenology under global warming. *Science*, 327(5972),  
664 1461–1462. <https://doi.org/10.1126/science.1186473>
- 665 Krinner, G., Viovy, N., de Noblet-Ducoudré, N., Ogée, J., Polcher, J., Friedlingstein, P.,  
666 Ciais, P., Sitch, S., & Prentice, I. C. (2005). A dynamic global vegetation model for  
667 studies of the coupled atmosphere-biosphere system. *Global Biogeochemical Cycles*,  
668 19(1), 1–33. <https://doi.org/10.1029/2003GB002199>
- 669 Lamarque, J. F., Dentener, F., McConnell, J., Ro, C. U., Shaw, M., Vet, R., Bergmann, D.,  
670 Cameron-Smith, P., Dalsoren, S., Doherty, R., Faluvegi, G., Ghan, S. J., Josse, B., Lee,  
671 Y. H., Mackenzie, I. A., Plummer, D., Shindell, D. T., Skeie, R. B., Stevenson, D. S., ...  
672 Nolan, M. (2013). Multi-model mean nitrogen and sulfur deposition from the  
673 atmospheric chemistry and climate model intercomparison project (ACCMIP):  
674 Evaluation of historical and projected future changes. *Atmospheric Chemistry and*  
675 *Physics*, 13(16), 7997–8018. <https://doi.org/10.5194/acp-13-7997-2013>

- 676 Laube, J., Sparks, T. H., Estrella, N., Höfler, J., Ankerst, D. P., & Menzel, A. (2014). Chilling  
677 outweighs photoperiod in preventing precocious spring development. *Global Change*  
678 *Biology*, 20(1), 170–182. <https://doi.org/10.1111/gcb.12360>
- 679 Luedeling, E., Girvetz, E. H., Semenov, M. A., & Brown, P. H. (2011). Climate change  
680 affects winter chill for temperate fruit and nut trees. *PLoS ONE*, 6(5).  
681 <https://doi.org/10.1371/journal.pone.0020155>
- 682 M. Stone. (1974). Cross-Validatory Choice and Assessment of Statistical Predictions.  
683 *Proceedings of the Royal Society B: Biological Sciences*, 36(2), 111–174.
- 684 Menzel, A., & Fabian, P. (1999). Growing season extended in Europe. *Nature*, 397(6721),  
685 659. <https://doi.org/10.1038/17709>
- 686 Niinemets, Ü., & Valladares, F. (2006). Tolerance to shade, drought, and waterlogging of  
687 temperate Northern Hemisphere trees and shrubs. *Ecological Monographs*, 76(4), 521–  
688 547.
- 689 Nishina, K., Ito, A., Falloon, P., Friend, A. D., Beerling, D. J., Ciais, P., Clark, D. B., Kahana,  
690 R., Kato, E., Lucht, W., Lomas, M., Pavlick, R., Schaphoff, S., Warszawski, L., &  
691 Yokohata, T. (2015). Decomposing uncertainties in the future terrestrial carbon budget  
692 associated with emission scenarios, climate projections, and ecosystem simulations using  
693 the ISI-MIP results. *Earth System Dynamics*, 6(2), 435–445. [https://doi.org/10.5194/esd-](https://doi.org/10.5194/esd-6-435-2015)  
694 [6-435-2015](https://doi.org/10.5194/esd-6-435-2015)
- 695 Piao, S., Tan, J., Chen, A., Fu, Y. H., Ciais, P., Liu, Q., Janssens, I. A., Vicca, S., Zeng, Z.,  
696 Jeong, S. J., Li, Y., Myneni, R. B., Peng, S., Shen, M., & Peñuelas, J. (2015). Leaf onset  
697 in the northern hemisphere triggered by daytime temperature. *Nature Communications*,  
698 6(APRIL). <https://doi.org/10.1038/ncomms7911>
- 699 Piñeiro, G., Perelman, S., Guerschman, J. P., & Paruelo, J. M. (2008). How to evaluate  
700 models: Observed vs. predicted or predicted vs. observed? *Ecological Modelling*, 216(3–  
701 4), 316–322. <https://doi.org/10.1016/j.ecolmodel.2008.05.006>

- 702 Polgar, C., Gallinat, A., & Primack, R. B. (2014). Drivers of leaf-out phenology and their  
703 implications for species invasions: Insights from Thoreau's Concord. *New Phytologist*,  
704 202(1), 106–115. <https://doi.org/10.1111/nph.12647>
- 705 Richardson, A. D., Black, T. A., Ciais, P., Delbart, N., Friedl, M. A., Gobron, N., Hollinger,  
706 D. Y., Kutsch, W. L., Longdoz, B., Luyssaert, S., Migliavacca, M., Montagnani, L.,  
707 Munger, J. W., Moors, E., Piao, S., Rebmann, C., Reichstein, M., Saigusa, N., Tomelleri,  
708 E., ... Varlagin, A. (2010). Influence of spring and autumn phenological transitions on  
709 forest ecosystem productivity. *Philosophical Transactions of the Royal Society B:*  
710 *Biological Sciences*, 365(1555), 3227–3246. <https://doi.org/10.1098/rstb.2010.0102>
- 711 Richardson, A. D., Hufkens, K., Milliman, T., Aubrecht, D. M., Furze, M. E., Seyednasrollah,  
712 B., Krassovski, M. B., Latimer, J. M., Nettles, W. R., Heiderman, R. R., Warren, J. M.,  
713 & Hanson, P. J. (2018). Ecosystem warming extends vegetation activity but heightens  
714 vulnerability to cold temperatures. *Nature*, 560(7718), 368–371.  
715 <https://doi.org/10.1038/s41586-018-0399-1>
- 716 Richardson, A. D., Keenan, T. F., Migliavacca, M., Ryu, Y., Sonnentag, O., & Toomey, M.  
717 (2013). Climate change, phenology, and phenological control of vegetation feedbacks to  
718 the climate system. *Agricultural and Forest Meteorology*, 169(FEBRUARY), 156–173.  
719 <https://doi.org/10.1016/j.agrformet.2012.09.012>
- 720 Schaber, J., & Badeck, F. W. (2003). Physiology-based phenology models for forest tree  
721 species in Germany. *International Journal of Biometeorology*, 47(4), 193–201.  
722 <https://doi.org/10.1007/s00484-003-0171-5>
- 723 Smith, B., Wärlind, D., Arneth, A., Hickler, T., Leadley, P., Siltberg, J., & Zaehle, S. (2014).  
724 Implications of incorporating N cycling and N limitations on primary production in an  
725 individual-based dynamic vegetation model. *Biogeosciences*, 11(7), 2027–2054.  
726 <https://doi.org/10.5194/bg-11-2027-2014>
- 727 Sykes, M. T., Prentice, I. C., & Cramer, W. (1996). *A Bioclimatic Model for the Potential*

- 728 *Distributions of North European Tree Species Under Present and Future Climates.*  
729 23(2), 203–233.
- 730 Taylor, K. E., Stouffer, R. J., & Meehl, G. A. (2012). An overview of CMIP5 and the  
731 experiment design. *Bulletin of the American Meteorological Society*, 93(4), 485–498.  
732 <https://doi.org/10.1175/BAMS-D-11-00094.1>
- 733 Templ, B., Koch, E., Bolmgren, K., Ungersböck, M., Paul, A., Scheifinger, H., Rutishauser,  
734 T., Busto, M., Chmielewski, F. M., Hájková, L., Hodzić, S., Kaspar, F., Pietragalla, B.,  
735 Romero-Fresneda, R., Tolvanen, A., Vučetič, V., Zimmermann, K., & Zust, A. (2018).  
736 Pan European Phenological database (PEP725): a single point of access for European  
737 data. *International Journal of Biometeorology*, 62(6), 1109–1113.  
738 <https://doi.org/10.1007/s00484-018-1512-8>
- 739 Tsallis, C., & Stariolo, D. A. (1996). Generalized simulated annealing. *Physica A: Statistical*  
740 *Mechanics and Its Applications*, 233(1–2), 395–406. [https://doi.org/10.1016/S0378-](https://doi.org/10.1016/S0378-4371(96)00271-3)  
741 [4371\(96\)00271-3](https://doi.org/10.1016/S0378-4371(96)00271-3)
- 742 Vitasse, Y. (2013). Ontogenic changes rather than difference in temperature cause understory  
743 trees to leaf out earlier. *New Phytologist*, 198(1), 149–155.  
744 <https://doi.org/10.1111/nph.12130>
- 745 Vitasse, Y., & Basler, D. (2013). What role for photoperiod in the bud burst phenology of  
746 European beech. *European Journal of Forest Research*, 132(1), 1–8.  
747 <https://doi.org/10.1007/s10342-012-0661-2>
- 748 Vitasse, Y., Schneider, L., Rixen, C., Christen, D., & Rebetez, M. (2018). Increase in the risk  
749 of exposure of forest and fruit trees to spring frosts at higher elevations in Switzerland  
750 over the last four decades. *Agricultural and Forest Meteorology*, 248(September 2017),  
751 60–69. <https://doi.org/10.1016/j.agrformet.2017.09.005>
- 752 Vitasse, Y., Signarbieux, C., & Fu, Y. H. (2017). Global warming leads to more uniform  
753 spring phenology across elevations. *Proceedings of the National Academy of Sciences*,

- 754 201717342. <https://doi.org/10.1073/pnas.1717342115>
- 755 Xiang, Y., Gubian, S., Suomela, B., & Hoeng, J. (2013). Generalized simulated annealing for  
756 global optimization: the GenSA Package. *R Journal*, 5(June), 13–28.  
757 <https://doi.org/10.1007/s10792-010-9404-x>
- 758 Yu, H., Luedeling, E., & Xu, J. (2010). Winter and spring warming result in delayed spring  
759 phenology on the Tibetan Plateau. *Proceedings of the National Academy of Sciences*,  
760 107(51), 22151–22156. <https://doi.org/10.1073/pnas.1012490107>
- 761 Zohner, C. M., Benito, B. M., Fridley, J. D., Svenning, J. C., & Renner, S. S. (2017). Spring  
762 predictability explains different leaf-out strategies in the woody floras of North America,  
763 Europe and East Asia. *Ecology Letters*, 20(4), 452–460.  
764 <https://doi.org/10.1111/ele.12746>
- 765 Zohner, C. M., Benito, B. M., Svenning, J. C., & Renner, S. S. (2016). Day length unlikely to  
766 constrain climate-driven shifts in leaf-out times of northern woody plants. *Nature*  
767 *Climate Change*, 6(12), 1120–1123. <https://doi.org/10.1038/nclimate3138>
- 768 Zohner, C. M., Mo, L., & Renner, S. S. (2018). Global warming reduces leaf-out and  
769 flowering synchrony among individuals. *ELife*.
- 770 Zohner, C. M., Mo, L., Renner, S. S., Svenning, J.-C., Vitasse, Y., Benito, B. M., Ordonez,  
771 A., Baumgarten, F., Bastin, J.-F., Sebald, V., Reich, P. B., Liang, J., Naburs, G.-J.,  
772 Miguel, S. de, Alberti, G., Antón-Fernández, C., Balazy, R., Brändli, U.-B., Chen, H. Y.  
773 H., ... Crowther, T. W. (2020). Late spring-frost risk between 1959 and 2017 decreased  
774 in North America, but increased in Europe and Asia. *Proceedings of the National*  
775 *Academy of Sciences*.
- 776 Zohner, C. M., Mo, L., Sebald, V., & Renner, S. S. (2020). Leaf-out in northern ecotypes of  
777 wide-ranging trees requires less spring warming, enhancing the risk of spring frost  
778 damage at cold range limits. *Global Ecology and Biogeography*.  
779 <https://doi.org/https://doi.org/10.1111/geb.13088>

780 Zohner, C. M., & Renner, S. S. (2014). Common garden comparison of the leaf-out  
781 phenology of woody species from different native climates, combined with herbarium  
782 records, forecasts long-term change. *Ecology Letters*, *17*(8), 1016–1025.

783 <https://doi.org/10.1111/ele.12308>

784 Zohner, C. M., & Renner, S. S. (2015). Perception of photoperiod in individual buds of  
785 mature trees regulates leaf-out. *New Phytologist*, *208*(4), 1023–1030.

786 <https://doi.org/10.1111/nph.13510>

787

### 788 **Acknowledgements**

789 This work was supported by grants to CMZ from the ETH Zurich Postdoctoral Fellowship  
790 program, LM from the China Scholarship Council, and TWC from DOB Ecology, Plant-for-  
791 the-Planet and the German Federal Ministry for Economic Cooperation and Development.

792 TAMP acknowledges funding from the European Research Council (ERC) under the European  
793 Union's Horizon 2020 research and innovation programme (grant agreement No 758873,  
794 TreeMort). This is paper number 45 of the Birmingham Institute of Forest Research.

795

### 796 **Author contributions**

797 The study was conceived and developed by CMZ. Statistical analysis was performed by LM  
798 and CMZ. LPJ-GUESS simulations were run by TAMP. The manuscript was written by CMZ  
799 with assistance from TWC. All other authors reviewed and provided input on the manuscript.

800

### 801 **Competing interest declaration**

802 The authors declare that there are no competing interests.

803

804

805



806 **Figure captions**

807

808 **Figure 1 | Testing for interactive climate effects on the timing of spring leaf-out.** **a**, In the  
809 *full model* (green), the amount of warming required to leaf-out is directly affected by winter  
810 chilling and the timing of spring onset (day length when spring warming occurs). In addition,  
811 winter chilling interacts with the timing of spring onset and autumn temperatures affect winter  
812 chilling accumulation. In the *Null model* (red), leaf-out is solely driven by spring warming. **b–**  
813 **d**, The interactive effects among climate factors should lead to an increase in warming  
814 requirements under warmer autumns (**b**), reduced chilling (**c**), and an earlier spring onset (**d**).  
815 **e**, Under cold spring conditions, leaf-out should occur earlier than expected from the *Null model*  
816 because long days and long chilling reduce the amount of warming required to leaf-out; under  
817 warm spring conditions, leaf-out should occur later than expected from the *Null model* because  
818 short days and short chilling increase the amount of warming required to leaf-out.

819

820 **Figure 2 | The effects of autumn temperature (a), winter chilling (b), and the timing of**  
821 **spring onset (c) on accumulated warming required to leaf-out.** Pearson correlation  
822 coefficients ( $\pm 2$  standard errors) are shown for each parameter. **a**, The mean temperatures of  
823 the months October and November, September to November, or September and October were  
824 used to calculate autumn temperatures. **b**, Two different temperature ranges were used to  
825 calculate winter chilling: all temperatures below 5°C (red) or temperatures between 0°C and  
826 5°C (turquoise). **c**, The relationship between the timing of spring onset (day length when spring  
827 warming occurs) and accumulated warming required to leaf-out. Number of analysed time-  
828 series per species: *Aesculus hippocastanum*, 3703; *Alnus glutinosa*, 1841; *Betula pendula*,  
829 3663; *Fagus sylvatica*, 3091; *Fraxinus excelsior*, 2178; *Larix decidua*, 2644; *Picea abies*, 2942;  
830 *Quercus robur*, 3152; *Tilia cordata*, 1436.

831

832 **Figure 3 | Leaf-out date predictions based on the empirical relationships between required**  
833 **accumulated warming and autumn temperature, winter chilling, and the timing of spring**  
834 **onset (see Figure 1).** **a, b**, Observed and empirically modelled leaf-out dates using 10-fold  
835 cross-validations in response to year (**a**) and spring temperature (**b**) averaged across all nine  
836 study species (observed leaf-out = black lines; *full model* = green lines; *chilling model* = blue  
837 lines; *Null model* = red lines). See Figs. S5 and S6 for species-specific plots. Loess smoothing  
838 curves in **b**) are based on random-effects models to control for differences among sites. **c**,  
839 Observed versus predicted leaf-out dates of the *full model*, the *chilling model*, and the *Null*

840 *model*. Solid lines show linear regression fit, dashed lines show the 1:1 line. For the *chilling*  
 841 *model* and the *Null model*, the intercept differed significantly from 0 and the slope differed from  
 842 1 ( $P < 0.05$ ). To standardize among sites, observed and predicted leaf-out dates are shown as  
 843 anomalies, i.e., as deviation from the mean observed leaf-out date at each site.

844

845 **Figure 4 | Model evaluation and future projections of Central European leaf-out dates. a–**  
 846 **c**, Model comparison of the three empirical models applied in this study (green = *full model*,  
 847 blue = *chilling model*, red = *Null model*) and 17 process-based models from the literature. **a**,  
 848 Significance values reporting whether the slope of observed versus predicted leaf-out dates  
 849 differs from 1. Numbers above indicate the percentages of sites for which the model slopes  
 850 were significantly ( $P < 0.05$ ) smaller (= overprediction) or larger than 1 (= underprediction). **b**,  
 851 Significance values reporting whether the intercept of observed versus predicted leaf-out dates  
 852 differs from 0. Numbers above indicate the percentages of sites for which the model intercepts  
 853 were significantly larger (= overprediction) or smaller than 0 (= underprediction). **c**, Root-  
 854 mean-square errors of models. The dashed line shows the average RMSE expected under a  
 855 Null-model where leaf-out dates do not differ among years. **d**, Future leaf-out projections (15-  
 856 year moving averages for nine species) under the RCP 8.5 climate-scenario, based on the seven  
 857 best performing models and the *Null model*. The grey area indicates one s.e. either side of the  
 858 mean. Right panel shows estimated advances in leaf-out by the end of the 21<sup>st</sup> century (2080–  
 859 2100) compared to the average leaf-out dates between 1990–2010 according to the *full model*  
 860 (green) and the *Null model* (red).

861

862 **Figure 5 | Effects of leaf-out changes in Northern Hemisphere temperate forests on net**  
 863 **primary productivity (NPP). a**, Annual forest NPP (above 23°N latitude) over the 21<sup>st</sup>  
 864 century, simulating spring leaf-out times with the *chilling model* (solid blue line) or the *full*  
 865 *model* (solid green line). Dashed lines show the baselines assuming no leaf-out changes in the  
 866 future (phenology fixed at years 2001–2010). **b**, Increases in NPP that are solely caused by leaf-  
 867 out shifts simulated with the *chilling model* and the *full model*. Arrows in a) and b) show the  
 868 cumulative difference in NPP between the standard LPJ-GUESS model (including the *chilling*  
 869 *model*) and the updated model (including our *full model*). **c**, Differences in average leaf-out  
 870 times of Northern Hemisphere temperate forests simulated with the *chilling model* and the *full*  
 871 *model*. Plant functional types: NS, needleleaved summergreen; BS, broadleaved summergreen  
 872 (either shade tolerant or intolerant).

873

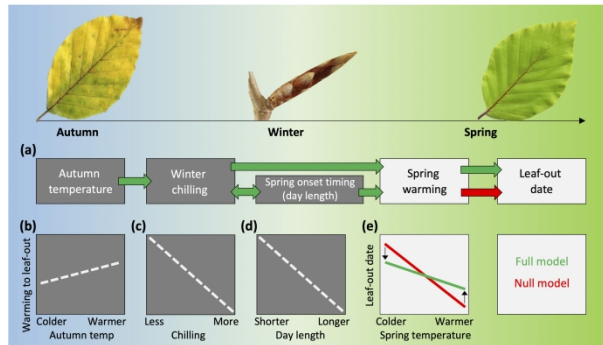


fig. 1

338x190mm (300 x 300 DPI)

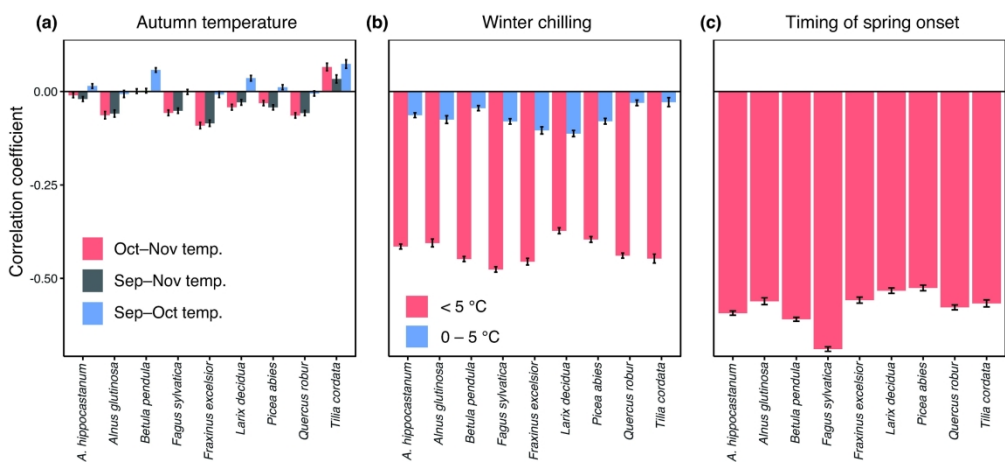


fig. 2

259x116mm (300 x 300 DPI)

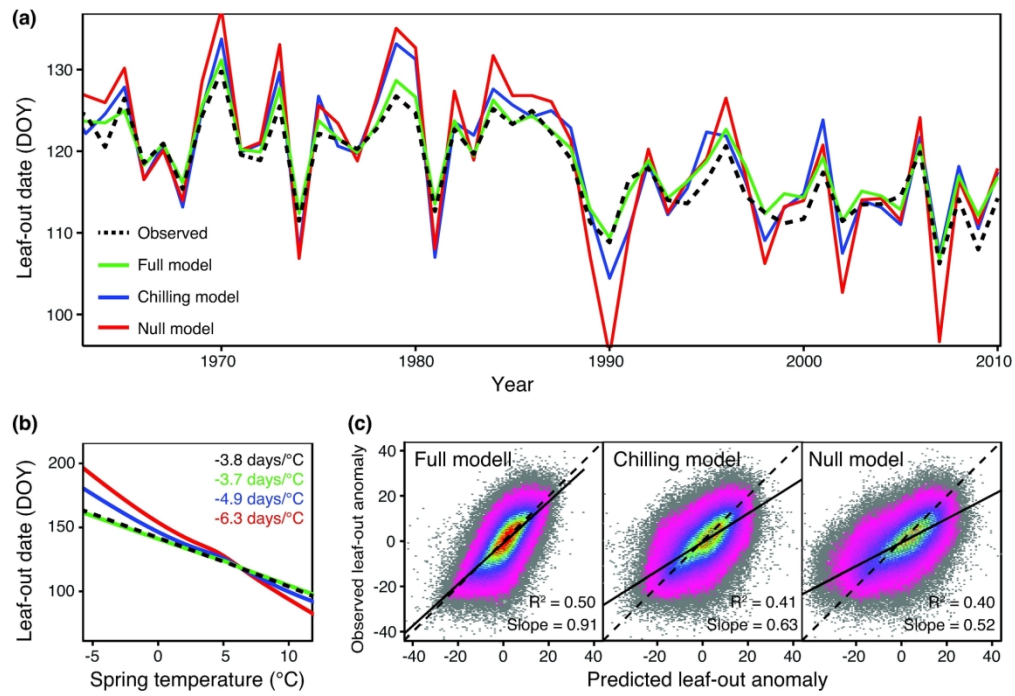


fig. 3

191x131mm (300 x 300 DPI)

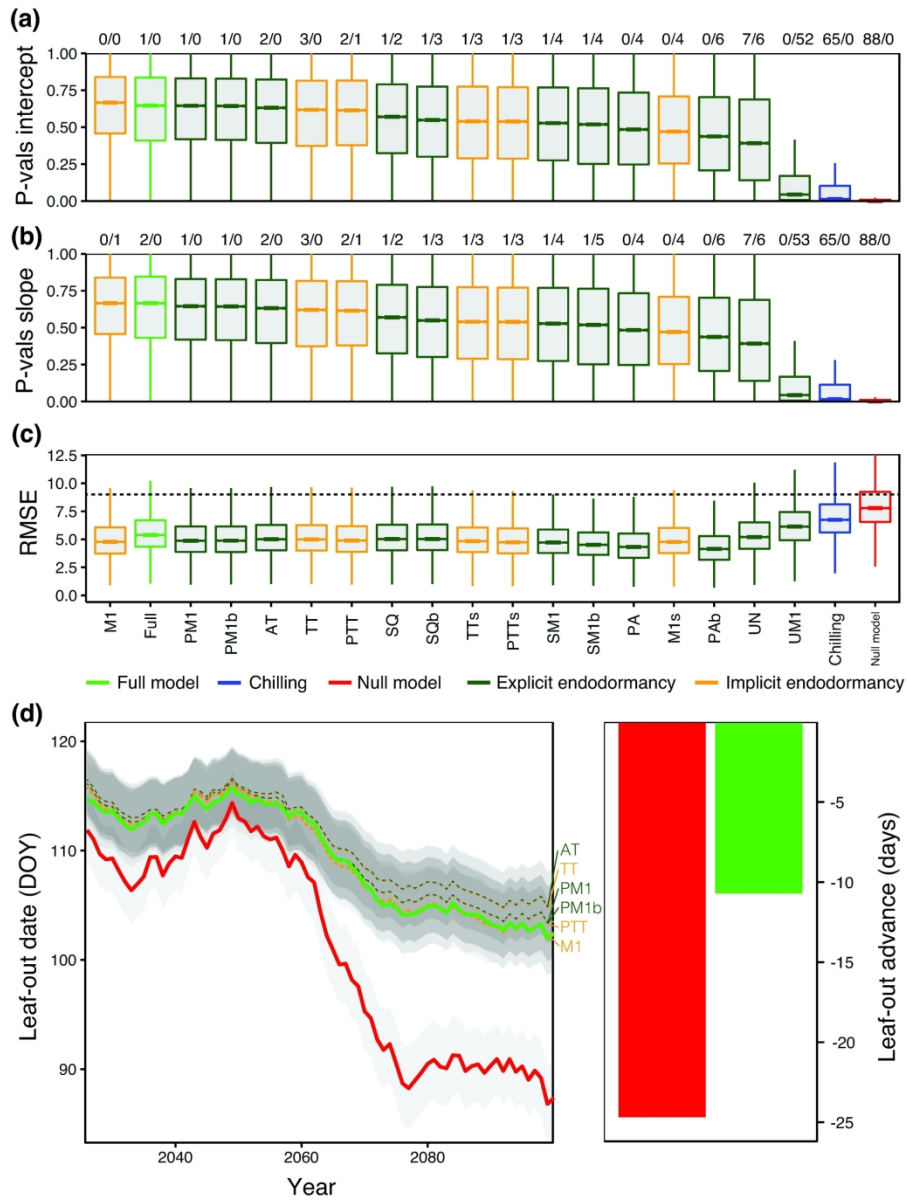


fig. 4

176x236mm (300 x 300 DPI)

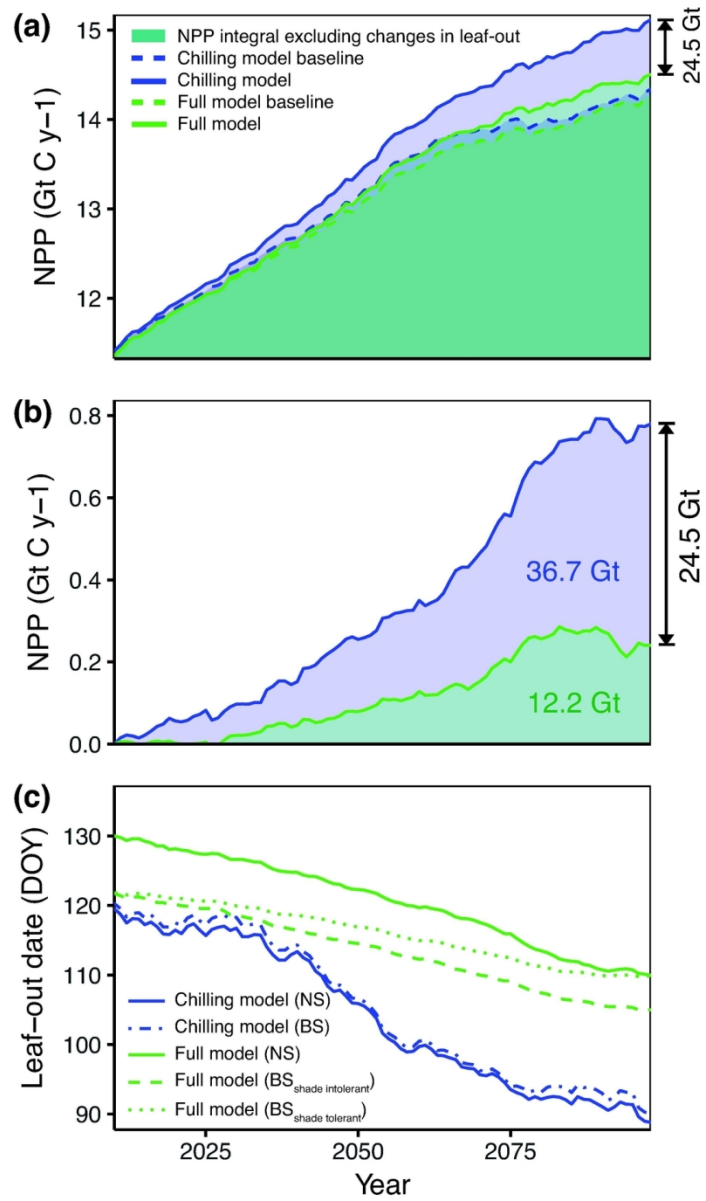


fig. 5

94x162mm (300 x 300 DPI)