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

3

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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⁻² (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 (“CO₂ 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 (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 (“CO₂ 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 21st 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 CO₂ 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 α , β , and κ 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 α , β , γ , and δ 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 CO₂ 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 CO₂ 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 ± 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 ± 0.2 days/°C. In contrast, the *chilling* and *null model*
383 over-estimated leaf emergence, predicting 4.9 ± 0.2 and 6.3 ± 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 21st 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 ~ 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 ~ 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 ± 0.1 days
477 per each degree increase in air temperature, predicting 3.7 ± 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 ± 0.2 and 6.3 ± 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 21st 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).

570

571

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787

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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.

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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 (± 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 21st 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 21st
 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

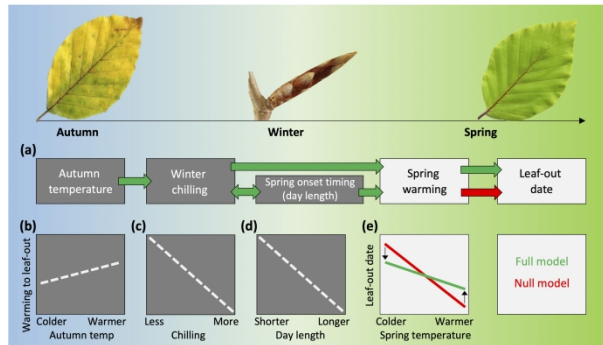


fig. 1

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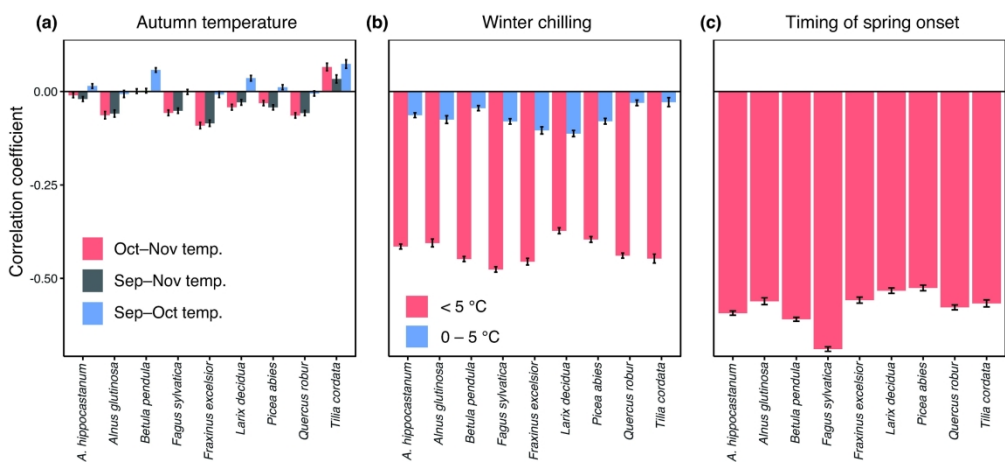


fig. 2

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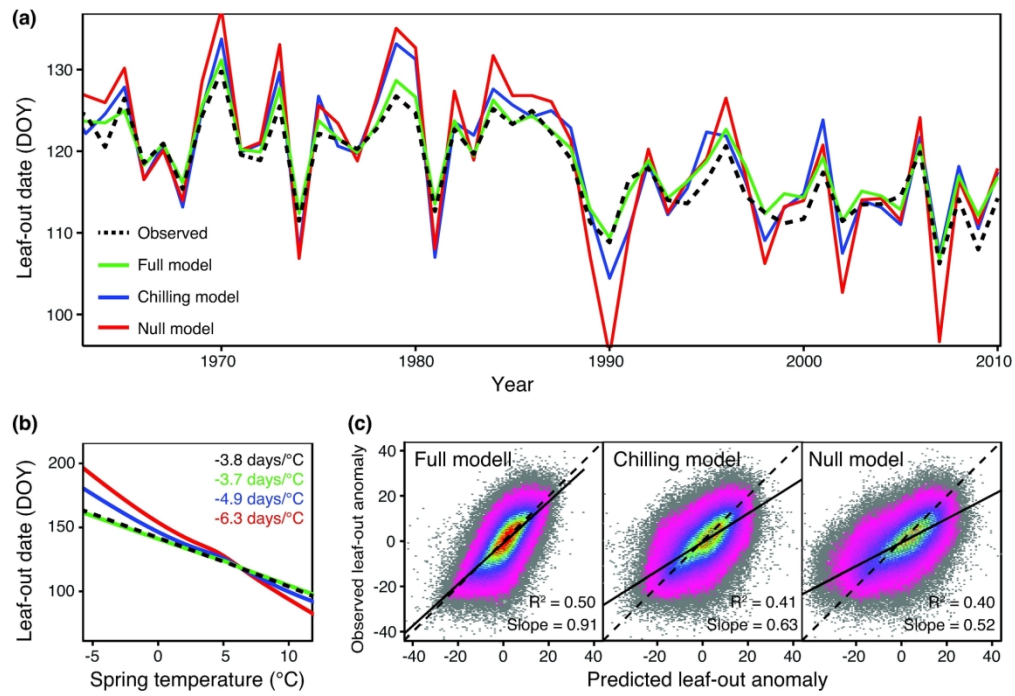


fig. 3

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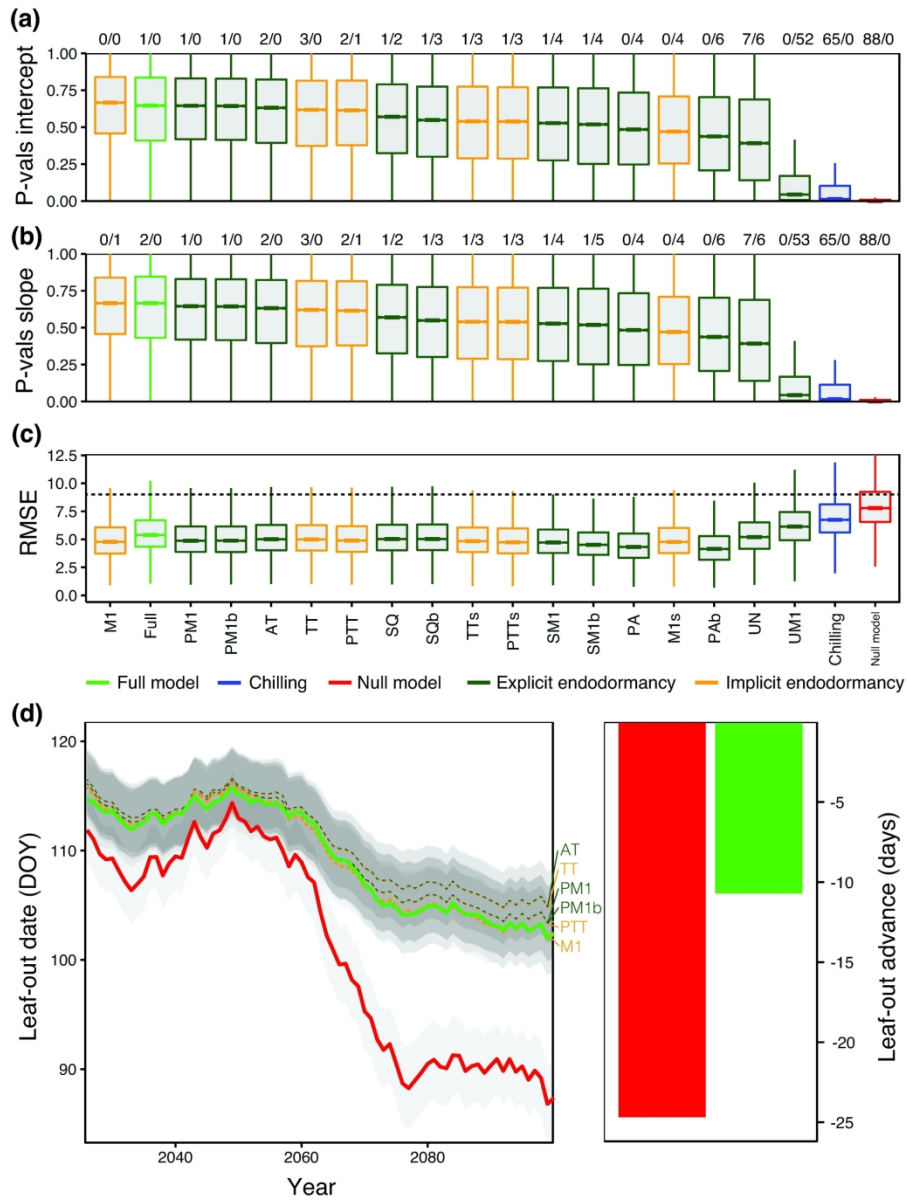


fig. 4

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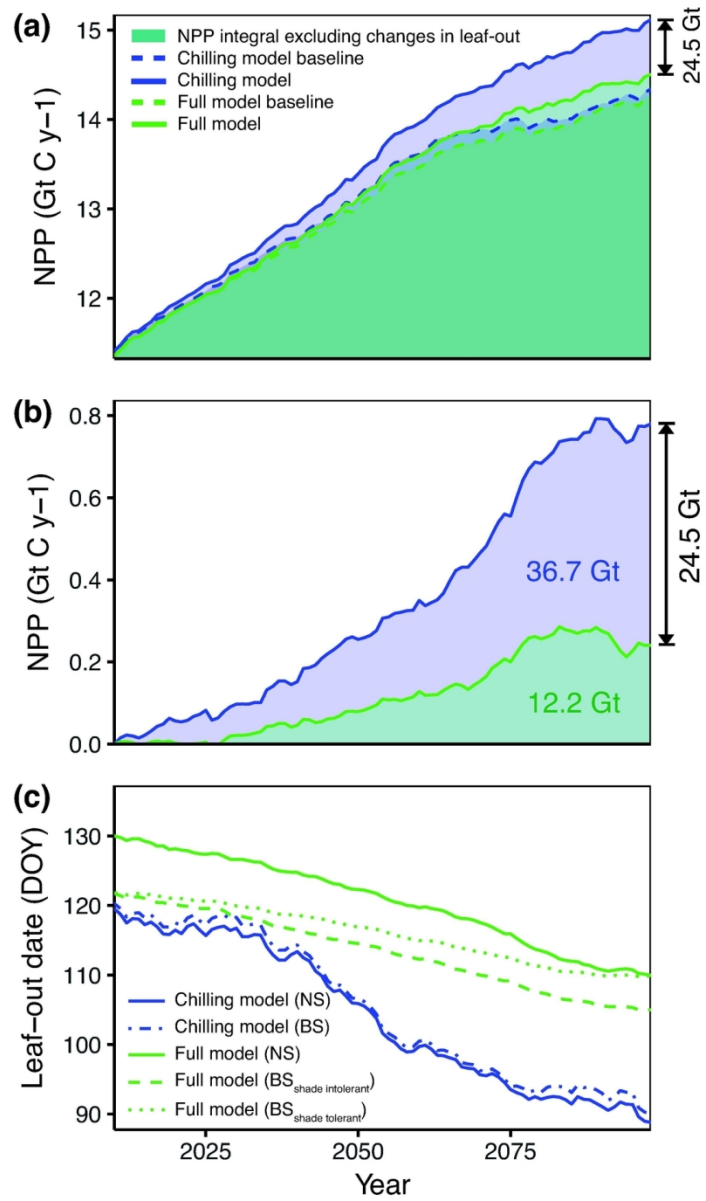


fig. 5

94x162mm (300 x 300 DPI)