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

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Abstract

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

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

Introduction

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

Three main factors — autumn temperatures (Fu et al., 2014; Heide, 2003), winter chilling (Laube et al., 2014; Luedeling et al., 2011; Yu et al., 2010; Zohner et al., 2017), and day length (Heide, 1993b, 1993a; Körner & Basler, 2010) — have been proposed to control spring leaf-out by modulating the amount of warming that trees require to leaf-out. These factors serve trees as a safety mechanism to prevent precocious leaf-out in case of an early warm spell when the risk of nightly freezing is still high (Körner & Basler, 2010; Zohner, Mo, Renner, et al., 2020; Zohner, Mo, Sebald, et al., 2020). Each of these factors is therefore likely to counteract the advances in spring onset under a warming climate. Specifically, as the climate warms, the accumulated warming required for leaves to emerge is expected to increase because: (i) warmer autumn temperatures delay the initiation of dormancy (Fu et al., 2014; Heide, 2003); (ii) warmer winters lead to reduced chilling accumulation (Fu et al., 2015; Zohner & Renner, 2014); and (iii) days at spring onset are becoming shorter (Fu et al., 2019a; Heide, 1993b; Vitasse & Basler, 2013; Zohner & Renner, 2015) (Fig. 1).

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

To represent the important phenological mechanisms into larger biogeochemical models, we need unifying evidence for the strength and direction of these ecological parameters. Empirically testing the influence of these environmental constraints is also vital for avoiding overparameterization in global biogeochemical models, which need to rely on simple sub-models to represent plant physiological processes. To date, dynamic global vegetation models, such as LPJ-GUESS, cannot reflect the complex dynamics that are represented in specialized phenology models. As such, they can only account for spring phenology using a simple degree-day–chilling relationship, neglecting the important physiological mechanisms that are likely to restrict the advance of spring phenology in the future. These models are thus likely to vastly overestimate the advances in spring phenology over the rest of the century. Addressing this huge source of uncertainty necessitates that we generate simple empirical parameters for the combined roles of autumn temperature, winter chilling and day length.

In this study, we aim to bridge the gap between specialized phenological models and global vegetation models by developing a simple, empirical model to evaluate the key mechanisms represented in process-based models. Using a massive *in situ* database of forest leaf-out observations, we determine the interactive effects of autumn temperature, winter chilling and spring day-length variation on thermal requirements to leaf-out in mature temperate forest trees. We then use the observed relationships to train statistical predictions of future spring arrival. By comparing this empirical model performance with all available process-based models from the phenological literature, we show that it adequately reflects the dominant drivers of spring phenology, and predicts spring leaf-out with as much accuracy as existing mechanistic models. In addition, we use forecasts of future temperatures to project the future changes in spring phenology under two climate change scenarios ("CO_2 stabilization" scenario, RCP 4.5 and "business-as-usual", RCP 8.5). With high confidence in our 'simple' empirical model performance, we could then use the calculated coefficients to train a global dynamic vegetation model to more accurately reflect the future changes in spring phenology. Ultimately, this big-data approach enables us to test the effects of interacting climate drivers, benchmark model projections, and evaluate how these mechanisms influence global dynamic vegetation model predictions of future phenology and global net primary productivity (NPP).

Methods

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

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

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

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

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

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

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

$$Chill_{hour} = 1 \quad if\ 0 \leq T \leq 5 \tag{2}$$

where chilling ($Chill_{hour}$) at any given time of the day depends on the temperature (T). We then calculated daily chilling proportions, e.g., a day in which in 75% of the time temperatures are between 0°C and 5 °C translates to 0.75 chilling days.

In addition, we calculated winter chilling including all temperatures below or equal to 5 °C (Fu et al., 2015) as:

$$Chill_{hour} = 1 \quad if\ T \leq 5 \tag{3}$$

To calculate the timing of spring onset for each year, we first needed to define a date reflecting the onset of spring warming. To do so, for each site and species combination, we calculated the average degree-days accumulating before leaf-out. Spring onset (SO) each year was then defined as the day length at the date when the average degree-days to leaf-out at the respective site were reached (Forsythe et al., 1995). SO thus reflects how early spring warming occurred each year.

$$\mathrm{SO} = 24 - \frac{24}{\pi} cos^{-1}\left[\frac{sin\frac{0.8333\pi}{180} + \sin\frac{L\pi}{180}\sin\varphi}{\cos\frac{L\pi}{180} * cos\varphi}\right] \tag{4}$$

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

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

where L is the latitude of the phenological site and DOY is the day of year when the average degree-days to leaf-out at each site were reached.

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

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

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

We used breakpoint analysis (Richardson et al., 2018), based on the residual sums of squares, to test whether the effect of the timing of spring onset or winter chilling on required accumulated warming is linear or whether the observed response is flattening beyond a threshold. In 70% and 76% of all time-series, a linear model was preferred over a breakpoint model for the effect of the timing of spring onset or winter chilling, respectively, on required accumulated warming. For the 30% and 25% of time series in which a breakpoint was inferred, we investigated whether steeper slopes are preferred with an earlier arrival of spring warming or decreasing chilling. For the timing of spring onset, a steeper slope at earlier dates was preferred for only 15% of pixels, while the opposite pattern also was preferred for 15% of pixels. For chilling, a steeper slope under low chilling was only inferred for 13% of pixels, while the opposite pattern was inferred for 11%. We thus rejected the hypothesis that the effect of the timing of spring onset or winter chilling on the amount of warming required to leaf-out is non-linear, i.e., increases with earlier arrival of spring warming or decreasing chilling.

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

By contrast to more complex phenological models, the starting date of degree-day accumulation was not fitted to the observed data and instead fixed to the first day of the year, allowing for easy incorporation into large-scale vegetation models. This also ensures that the *null model* (warming-only model) is not confounded by other factors because fitting a starting date of degree-day accumulation implicitly accounts for winter chilling and/or day-length by determining when plants become susceptible to spring warming.

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

Process-based phenological models

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

Model evaluation

To judge the performance of phenological models, previous studies relied either solely on root-mean square errors (RMSEs) of observed vs predicted leaf-out dates (Basler, 2016; Fu et al., 2012; Vitasse et al., 2018) or additionally evaluated model predictions by comparing predicted (in the y-axis) vs observed (in the x-axis) leaf-out dates (Delpierre et al., 2009; Hufkens et al., 2018; Schaber & Badeck, 2003). However, such regression to evaluate models is incorrect, leading to erroneous estimates of the slope and intercept (Piñeiro et al., 2008). Especially in directional models such as spring phenological projections, where future climate conditions will lead to ever earlier occurrence dates, models need to be evaluated by analyzing intercept and slope components of observed (in the y-axis) vs predicted dates (in the x-axis). To do so, we conducted Wald-test based comparisons (Fox, 2016) using the linearHypothesis function in the R-package car, allowing us to test for each individual site whether the slopes and intercepts of observed *vs.* predicted leaf-out dates differ significantly from 1 and 0, respectively (Fig. 4a,b). For each species, we also obtained the overall model fit (R^2 values) and RMSEs for observed *versus* predicted values (Figs. 3c, 4c, and S4). Next, we applied 10-fold cross-validations (M. Stone, 1974), and tested whether projected leaf-out dates capture (i) observed temporal trends and (ii) the observed sensitivity of leaf-out dates to spring temperatures (Figs. 3a,b, S5, and S6). To calculate temperature sensitivity trends based on time-series, we had to remove noise that is due to between-site variation. This was done by adjusting the data using mixed effects modelling available through the R-package lme4.

Future projections of spring onset

To examine how the analysed ecological mechanisms influence future projections of spring leaf-out, we extrapolated the timing of spring leaf-out until 2100 using two future climate scenarios ("CO_2 stabilization" scenario, RCP 4.5 and "business-as-usual", RCP 8.5; Fig. S7). Specifically, for each scenario, we ran statistical extrapolations of future leaf-out dates, based on the seven best-performing phenology models, including our *full model*, and the simple *null model* accounting solely for temperature accumulation. Future projections of daily minimum and maximum temperatures came from (Beer et al., 2014) (Fig. S7). Emissions in the RCP 4.5 climate scenario peak around 2040 and then decline. In the RCP 8.5 climate scenario emissions continue to rise throughout the 21st century.

Land-surface flux projections

We used LPJ-GUESS, a dynamic global vegetation model (Smith et al., 2014), to simulate the effects of shifting spring phenology on temperate forest net primary productivity (NPP). LPJ-GUESS represents vegetation growth and dynamics using a mixture of plant functional types that respond to forcing from the climate (temperature, precipitation, incoming shortwave radiation), atmospheric CO_2 mixing ratios and soil type. The successional structure of vegetation is simulated using multiple (here ten) replicate patches in each grid cell, which are subject to stochastic processes of establishment and mortality. Photosynthesis, respiration, stomatal conductance and phenology in LPJ-GUESS are simulated on a daily time step.

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

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

where C is the length of the chilling period and α, β, and κ are constants specific to plant functional types.

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

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

where C is the length of the chilling period, D is the timing of spring warming, CD is the interaction between chilling and the timing of spring warming, and α, β, γ, and δ are coefficients specific to plant functional types (table S1). The length of the chilling period was defined as the number of days <5°C from 1 October, the timing of spring warming was defined relative to a degree-day threshold (table S1). We calculated a specific spring onset for each functional type because, the needleleaf summergreen species *Larix decidua*, for example, flushes earlier than many broadleaf summergreen trees. Three functional types of trees (BSI, broadleaved summergreen shade-intolerant; BST, broadleaved summergreen shade-tolerant; NS, needleleaved summergreen) were present in our species sampling. Following (Niinemets & Valladares, 2006), *Fagus sylvatica* and *Tilia cordata* were treated as shade tolerant, *Aesculus hippocastanum*, Alnus glutinosa, *Betula pendula*, *Fraxinus excelsior*, and *Quercus robur* as shade intolerant. Leaf-out phenology of *Picea abies* was not included in LPJ-GUESS because, in evergreen species, onset of photosynthetic activity in spring is not dependent on the flushing of new buds. In addition to the deciduous plant functional types described above, LPJ-GUESS simulations also included a temperate needleleaved evergreen tree, a boreal needleleaved evergreen shade-tolerant tree, a boreal needleleaved evergreen shade-intolerant tree and a C3 grass (Smith et al., 2014), with the distributions of each functional type governed by model-internal processes of competition. All simulations were run as potential natural vegetation (i.e. without land management) and the outputs were masked and rescaled to current temperate forest area as defined by (Hansen et al., 2013).

Daily climate forcing data came from the r1i1p1 ensemble member of the IPSL-CM5A-LR model from CMIP5 (Taylor et al., 2012) for 1850-2099 following the RCP 8.5 scenario, bias-corrected to 1960-1999 WATCH climate (Hempel et al., 2013), as prepared for the ISI-MIP2 project. Atmospheric CO_2 mixing ratios were as prescribed for the RCP 8.5 scenario of CMIP5 and N deposition data was taken from Lamarque et al. (Lamarque et al., 2013). Simulations were spun-up for 500 years using recycled, detrended 1850-1879 climate, and 1850 atmospheric CO_2 mixing ratio and N deposition. They were then run under fully transient environmental forcings from 1850-2099. The spatial resolution was 0.5° x 0.5°. In total four simulations were conducted: simulations with the original and updated phenology algorithms, and two further simulations in which, for each of the algorithms, leaf out dates from 2010 onwards were forced by mean 2001-2010 daily temperatures in each grid cell, so as to provide a baseline from which to identify the effects of the phenology algorithm on the carbon cycle.

Results

The environmental drivers of spring leaf-out

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

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

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

Evaluating phenology model performance

Compared to all existing phenology models, our empirical model performed well in predicting leaf emergence over the last 15 years of leaf-out observations, explaining over 50% of the variation in spring leaf emergence over 727,401 observations. This was only marginally worse explanatory power than the best available phenology models (see RMSE values in Fig. 4c). Our *full model* also showed high model-accuracy, with predictions fitting close to the 1:1 line in predicted *vs.* observed plots (Fig. 4c). As such, the intercept and slope components of observed *vs.* predicted comparisons of leaf-out dates for our *full model* were among the least likely to differ from 1 and 0, respectively, with a significant (P <0.05) deviation only found for <2% of sites (Fig. 4 a,b). Four of the other process-based models showed an equally low proportion of significant sites with exceptionally high model accuracy. Model accuracy was slightly lower for 11 models (2–6% significant sites), while the remaining 4 models all performed considerably worse (13–88% significant sites) [Fig. 4 a,b]. The best-performing model was the M1 model both in terms of model explanatory power and accuracy.

Future projections of spring leaf-out

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

Changes in temperate forest productivity

The standard LPJ-GUESS model (including a simple chilling–degree-day function to predict spring phenology) estimated that, under a "business-as-usual" climate-scenario, earlier spring arrival will enhance NPP of temperate forests by ~0.8 Gt carbon per year at the end of the century, resulting in a total increase of cumulative spring NPP of 37 Gt carbon over the rest of the century. In contrast, the updated model, including the new empirically-derived information about the ecological constraints on spring phenology (table S1), estimated that earlier spring arrival will enhance NPP of temperate forests by only ~0.2 Gt per year at the end of the century, resulting in a total increase of only 12 Gt over the rest of the century (Figure 5).

Discussion

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

While our findings suggest that the timing of the onset of spring warming, represents a strong control on leaf emergence across all nine studied tree species (see Fu *et al.* (2019b) for a more detailed test of this relationship), it remains unclear what is ultimately driving this relationship. A possible explanation for the negative relationship between the amount of warming required to leaf-out and the ‘earliness’ of spring onset is day length. Yet, experimental studies revealed that only in a few species, such as *Fagus sylvatica*, does day length have an effect on spring leaf-out timing (Laube et al., 2014; Zohner et al., 2016). It is therefore also possible that the time effect we detect here could ultimately be driven by mechanisms other than day length, such as time *per se* (sensed through an internal clock) or changes in spectral light composition (Brelsford & Robson, 2018). Our results do not give mechanistic insights that would allow us to disentangle the mechanisms by which plants sense the time of the year, but they provide important evidence that both winter chilling and the timing of the onset of spring warming modulate the amount of warming required to leaf-out, thereby restricting future advances in leaf emergence under climate change.

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

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

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

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

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

Our simple empirical model was trained on current climate conditions, which can lead to uncertainties in future projections if environmental conditions fall outside the model training range. Yet, as expected from the high predictive accuracy of the top models, the seven best models gave very similar future predictions, with our *full model* and the best-performing M1 model representing the same leaf-out trajectories (Fig. 4d). Compared to our *null model*, in which spring warming was the sole driver of leaf-out phenology, the top models estimated a ~60% or 14 days reduction in the phenological responses to global warming (Fig. 4d). This demonstrates that, despite different parameters and assumptions, there is a broad consensus among phenology models – including our *full model* . As such, our simple regression model can serve to provide basic parameters that can easily be incorporated into large-scale vegetation models and Earth system models to project future terrestrial vegetation carbon dynamics. More complex phenological models rely on spatially-explicit parameter-optimization algorithms to account for endodormancy release. Capturing the spatial variation across temperate forests would require large amounts of spatially-uniform phenological data to train these models. Such data does not currently exist and would require a huge coordinated sampling effort. In contrast, our regression model offers a highly parsimonious approach, reflecting the main mechanisms triggering spring phenology without the limitations of model overparameterization. This approach can therefore provide projections of increased veracity without inflating structural uncertainty, which remains the main cause of divergence in vegetation model projections (Nishina et al., 2015). Our model can thus provide the empirical relationships that are needed to underpin future projections of temperate spring phenology, and its impacts on terrestrial vegetation carbon dynamics.

To finally comprehend how our leaf-out predictions will affect future projections of NPP, we used a dynamic global vegetation model (LPJ-GUESS). Previously, spring phenology was implemented as a function of degree-days and winter chilling (see *chilling model* in Figs. 3, 4, and 5) (Sykes et al., 1996). We parameterized the phenology algorithm using the empirically-derived relationships with the timing of spring onset, and the updated estimates of winter chilling (table S1). These changes drastically reduced the projected increases in temperate forest productivity over the rest of this century. Specifically, the standard LPJ-GUESS model (including chilling-only) estimates that cumulative temperate forest NPP will increase over the rest of the century by a total of 37 Gt carbon as a result of earlier spring onset. However, the updated model, including the new empirically-derived information about the ecological constraints on spring phenology estimates an increase of only 12 Gt over the same time period (Figure 5). These differences highlight the need for an improved representation of plant phenology when predicting vegetation dynamics and the terrestrial carbon cycle. The high predictive accuracy of state-of-the-art phenology models we detect here demonstrates that it is possible to adequately represent the main environmental drivers of phenology and future efforts should thus be directed toward integrating these relevant drivers within boreal, temperate, and tropical ecosystems in global vegetation models.

Conclusions

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

Data deposition statement

All data used for this study is freely available through the Pan European Phenology project (www.PEP725.eu).

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Author contributions

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

Competing interest declaration

The authors declare that there are no competing interests.

Figure captions

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

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

Figure 3 | Leaf-out date predictions based on the empirical relationships between required accumulated warming and autumn temperature, winter chilling, and the timing of spring onset (see Figure 1). a, b, Observed and empirically modelled leaf-out dates using 10-fold cross-validations in response to year (**a**) and spring temperature (**b**) averaged across all nine study species (observed leaf-out = black lines; *full model* = green lines; *chilling model* = blue lines; *Null model* = red lines). See Figs. S5 and S6 for species-specific plots. Loess smoothing curves in b) are based on random-effects models to control for differences among sites. **c**, Observed versus predicted leaf-out dates of the *full model*, the *chilling model*, and the *Null* *model*. Solid lines show linear regression fit, dashed lines show the 1:1 line. For the *chilling model* and the *Null model*, the intercept differed significantly from 0 and the slope differed from 1 ($P < 0.05$). To standardize among sites, observed and predicted leaf-out dates are shown as anomalies, i.e., as deviation from the mean observed leaf-out date at each site.

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

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

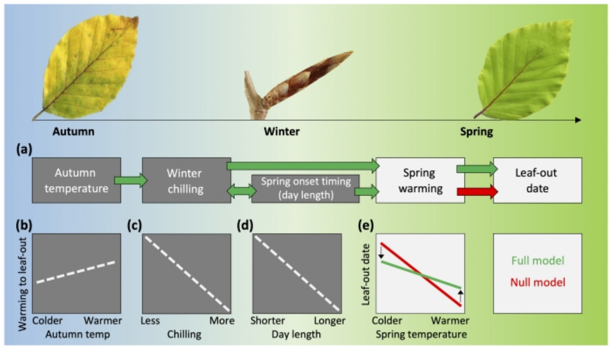

fig. 1

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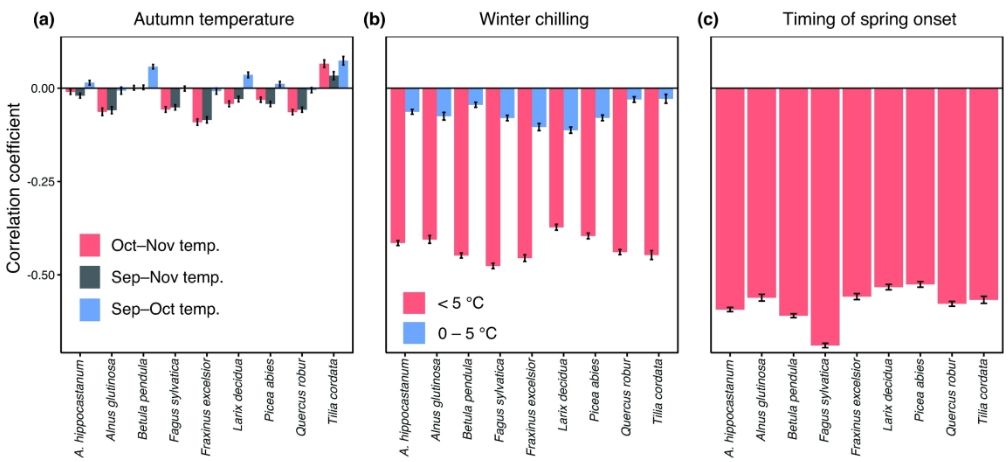

fig. 2

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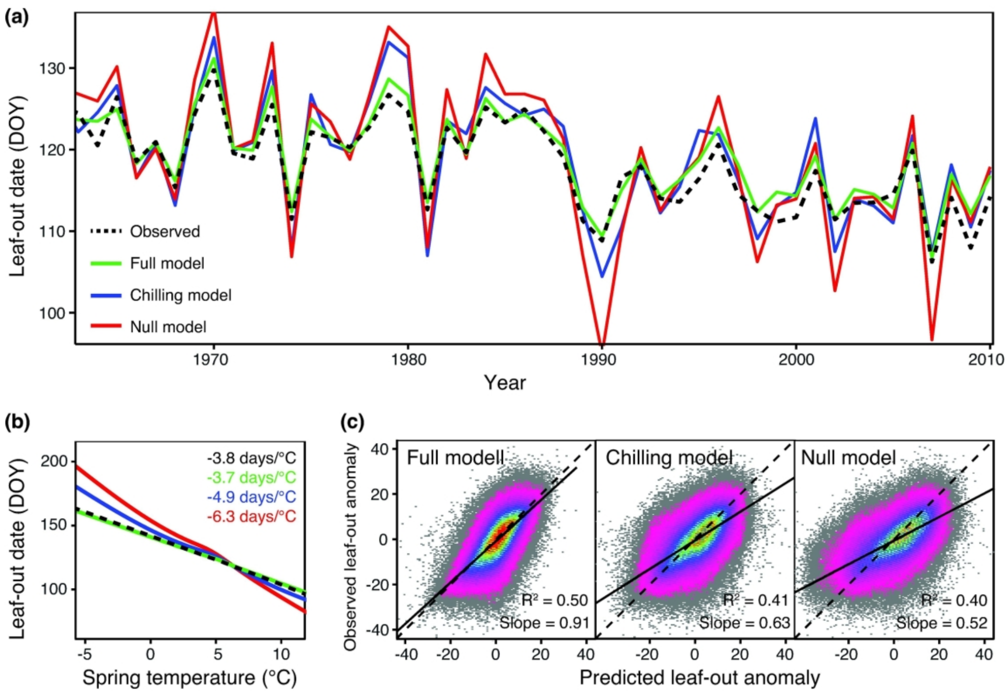

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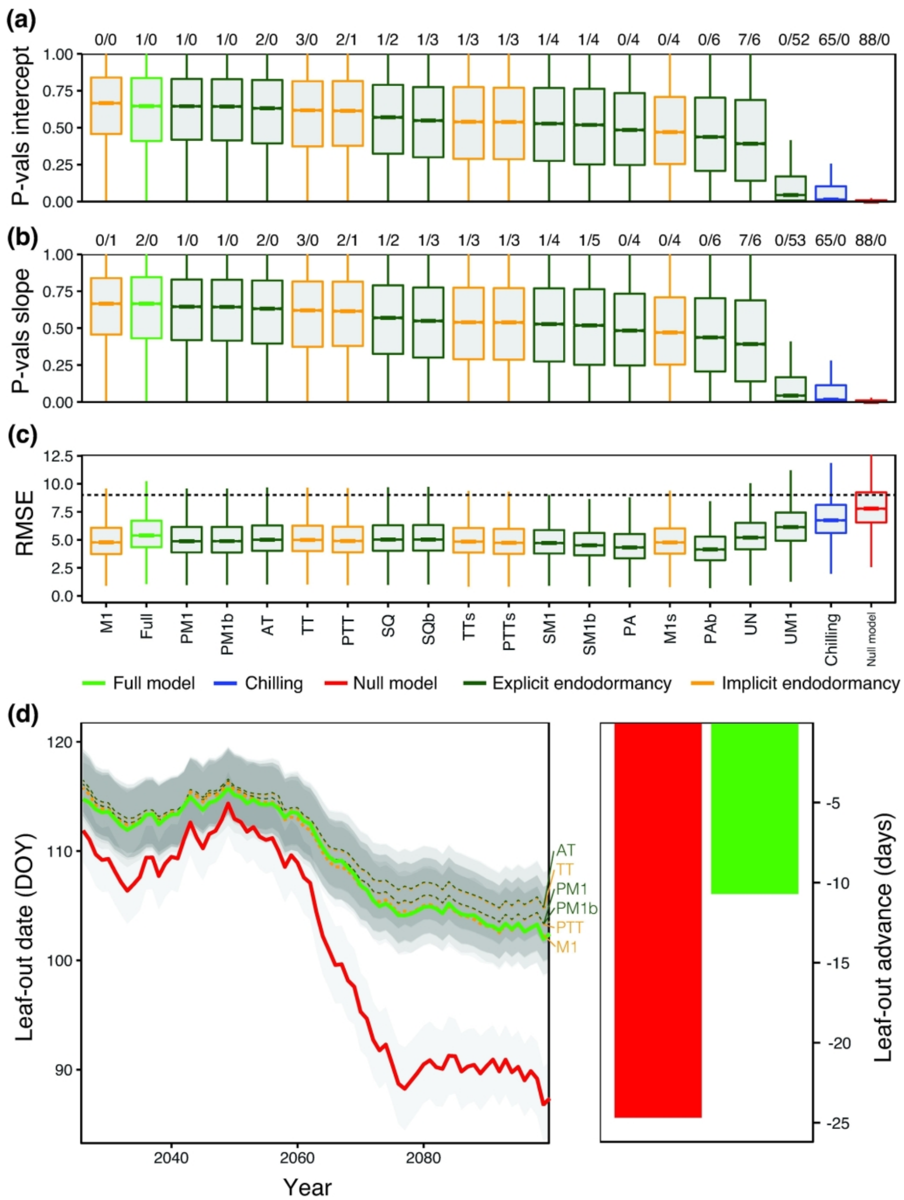

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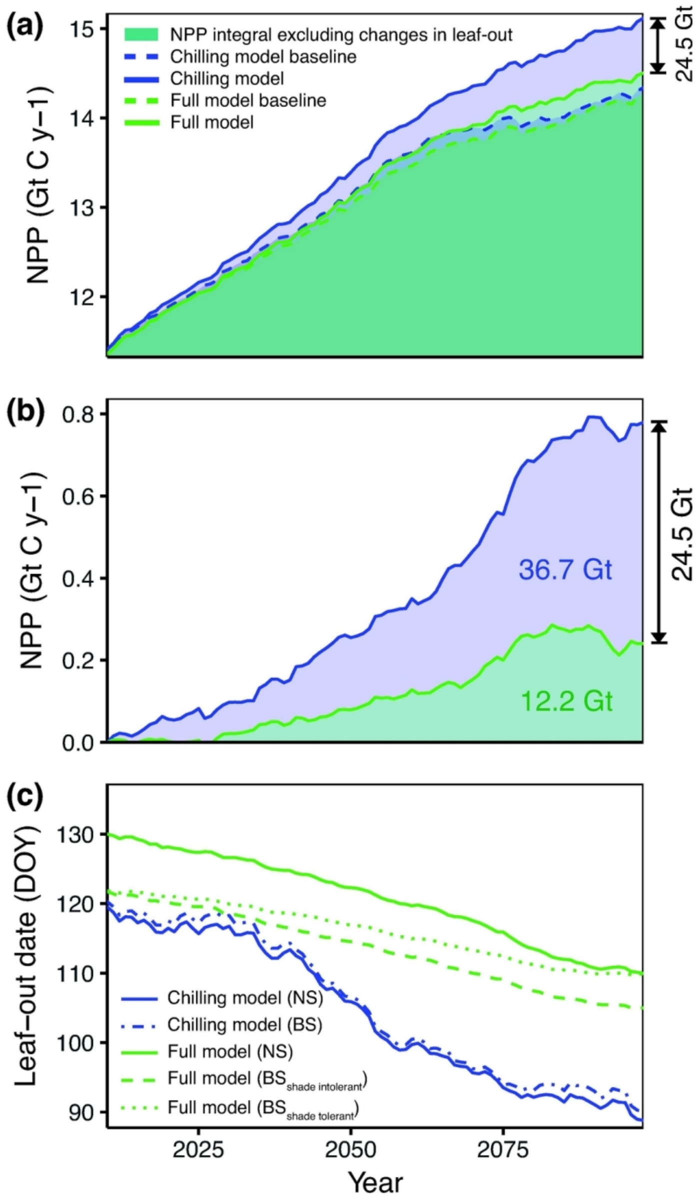

fig. 5

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