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Diverging models introduce large uncertainty in future climate warming impact on spring phenology of temperate deciduous trees

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Abstract

Spring phenology influences terrestrial ecosystem carbon, water and energy exchanges between the biosphere and atmosphere. Accurate prediction of spring phenology is therefore a prerequisite to foresee the impacts of climate warming on terrestrial ecosystems. In the present study, we studied the model performance of four widely used process-based models of spring leaf unfolding, including both a one-phase model (not considering a chilling phase: the Thermal Time model) and three two-phase models (all accounting for a required chilling period: the Parallel model, the Sequential model, the Unified model). Models were tested on five deciduous tree species occurring across Europe. We specifically investigated the divergence of their phenology predictions under future climate warming scenarios and studied the differences in the chilling periods. We found that, in general, the two-phase models performed slightly better than the one-phase model when fitting to the observed data, with all two-phase models performing similarly. However, leaf unfolding projections diverged substantially among the two-phase

models over the period 2070-2100. Furthermore, we found that the modeled end dates of the chilling periods in these models also diverged, with advances for both the Sequential and Parallel models during the period 2070-2100 (compared to the period 1980-2010), and delays in the Unified model. These findings thus highlight large uncertainty in the two-phase phenology models and confirm that the mechanism underlying the leaf unfolding process is not yet understood. We therefore urgently need an improved understanding of the leaf unfolding process in order to improve the representation of phenology in terrestrial ecosystem models.

Keywords: climate warming, phenology models, leaf unfolding, chilling period, Europe, uncertainty

1. Introduction

Climate change has substantially affected terrestrial ecosystem structure and functions (Walter *et al.*, 2002). The ecological effects of climate change are already clearly observed in phenology (Fu *et al.*, 2015; Menzel *et al.*, 2006a; Walther *et al.*, 2002), but also in altered composition and population dynamics of ecosystems worldwide (Chuine, 2010; Diez *et al.*, 2012; Migliavacca *et al.*, 2012; Parmesan & Hanley, 2015; Scheffers *et al.*, 2016; Vitasse *et al.*, 2011). Spring phenology defines the onset and duration of growing season (Richardson *et al.*, 2013; Schwartz, 2013), thus strongly impacts on the primary productivity of terrestrial ecosystems (Piao *et al.*, 2007; Richardson *et al.*, 2010), as well as their water balance (Lian *et al.*, 2020). In addition, the timing of phenological events co-determines species distributions (Chuine, 2010), and the order of phenological timings among species determines the structure and composition in plant

communities (Cleland *et al.*, 2007; Rathcke & Lacey, 1985). Therefore, accurately predicting and assessing phenology dynamics is crucial to improve our understanding of ecosystem responses to the ongoing climate change (Piao *et al.*, 2019).

Many studies have shown that the period before leaf unfolding plays a determinant role in the leaf unfolding process, and this period during which plants respond strongly to warm temperatures is generally called ecodormancy (Lang *et al.*, 1987; Baček *et al.*, 2004; Landsberg, 1974; Menzel *et al.*, 2006a; Sarvas, 1972; White *et al.*, 1997). Based on this finding, the Thermal Time model, a so-called one-phase model, was developed and widely applied in dynamic global vegetation models (Botta *et al.*, 2000; Richardson *et al.*, 2013). This simple one-phase model supposed that the leaf unfolding is determined only by warm temperatures forcing bud break. Once the forcing temperatures have accumulated above a forcing threshold (the heat requirement), leaves start to unfold (Arnold, 1959; Cannell & Smith, 1983; Réaumur, 1735; Wang, 1960). However, many studies have found that other environmental variables, such as accumulation of cold temperatures (chilling) during winter, day-length, and precipitation also influence the heat requirement (Basler & Körner, 2012, 2014; Cannell & Smith 1983; Fu *et al.*, 2014b; Fu *et al.*, 2015; Fu *et al.*, 2019; Heide, 1993; Murray *et al.*, 1989; Richardson *et al.*, 2013). Hence, the models involving other factors are often more accurate in reproducing observed phenology dynamics (Basler *et al.*, 2016; Fu *et al.*, 2012b; Vitasse *et al.*, 2011). However, the mechanisms through which these other environmental factors co-regulate the leaf unfolding process remain unclear, mainly due to limited understanding of the dormancy process (Chuine *et al.*, 2016; Hänninen, 2016).

During dormancy, the buds of trees first enter into a rest state, a phase that is called endodormancy (Lang *et al.*, 1987). During this phase, the cells of the meristems switch to an offline state with no potential for growth, and become sensitive to low temperatures (hereafter called chilling). Chilling promotes the digestion of certain enzymes and reopens the pathways for cell-to-cell communication (Rinne *et al.*, 2001). A certain amount of chilling (hereafter called the chilling requirement) results in the break of endodormancy, upon which the meristems enter into the ecodormancy phase. It is worth noting that there is a limited temperature range in which the chilling effect accumulates. If temperature is lower than the minimum value for chilling, meristem cells produce antifreeze proteins and modify membranes to tolerate the freezing temperature (Heber *et al.*, 1979; Larcher, 2005; Vitasse *et al.*, 2014; Wisniewski *et al.*, 2014). Very low temperatures therefore do not contribute to fulfilling the chilling requirement. Considering that the temperature ranges for chilling vary among species and locations, and cannot be determined empirically, it is difficult to establish the day when the chilling requirement has been reached (Caffarra & Donnelly, 2011a; Falusi & Calamassi, 1990). Furthermore, even the sequence of the chilling and forcing phases is still equivocal. Some experimental studies have suggested that forcing temperatures do not start to accumulate until the chilling requirement has been fulfilled (Hänninen, 1990; Kramer, 1994), whereas other studies have shown that chilling and forcing temperatures accumulate in parallel (Hänninen, 1990; Kramer, 1994; Landsberg, 1974). Based on these contrasting findings, different chilling-forcing-based models, the so-called two-phase models, have been developed (Hänninen, 1990; Chuine, 2000).

Accurate projections of climate change require accurate assessment of vegetation feedbacks that, in turn, depend on accurate predictions of spring phenology to climate warming. Relevant questions arising are how spring phenology will change under different climate scenarios and how strongly do the various existing phenology models differ in their projected responses to climate warming? With these questions in mind, we fitted both one-phase and two-phase models to observations of leaf unfolding dates over the past three decades during which climate warmed substantially in Europe. Therefore, from this large available data pool, we selected 30% of the years (those with the warmest winters) to parameterize the models. After assessing the model performance under these warm winters in the current climate, we then investigated the divergence of their phenology predictions under future climate warming conditions. This study thus calibrates multiple phenology models to the observations under current day warm conditions and assesses to what degree their predictions of spring phenology and the end dates of chilling accumulation diverge in a future, warmer climate.

2. Materials and method

2.1 Phenological observations

To test the model performances under current-day conditions, we collected a large set of phenological observations. First leaf unfolding dates (FLU) defined by the BBCH (Biologische Bundesanstalt, Bundessortenamt and Chemical Industry) code 11 (Meier, 1997) were obtained from the Pan European Phenology Database, which is an open and unrestricted-access database of 139 plant species and 33 growth stages across 30 European countries (<http://www.pep725.eu/>). We selected the following tree species because they had high data availability in the database:

Alnus glutinosa (mean FLU: 107 ± 8), *Betula pendula* (108 ± 6), *Fagus sylvatica* (116 ± 6), *Fraxinus excelsior* (127 ± 7), and *Quercus robur* (123 ± 7). After excluding outliers of FLU later than June (180 DOY: day of the year) that may have been incorrectly recorded, in total 1208 sites (Fig. A.1) and 4087 species-sites combinations were selected, each with at least 25 observation years over the period 1980-2012. Note that these phenology observations were only from Central Europe, i.e. mainly Germany, Austria, Slovenia and Croatia.

2.2 Climate data

Daily mean air temperature data over the period 1979-2012 was collected from the WATCH Forcing Data methodology applied to ERA-Interim data (WFDEI). It is a bias-corrected re-analysis dataset of meteorological variables which covers global land including Antarctica with a spatial resolution of 0.5° by 0.5° (Piani *et al.*, 2010; Weedon *et al.*, 2014). In addition, a station-based climate dataset (1979-2012), i.e. European Climate Assessment & Dataset (ECAD, <http://www.ecad.eu/>), was also used to fit each phenology model. After excluding the phenology sites located more than 30 km from the nearest climate measurement site, 734 sites (~61% of 1208 sites) remained to fit the phenology models. 86% of these phenology sites were less than 15 km from the nearest climate measurement site.

For the future phenology predictions over the period 2069-2100, we used three temperature datasets from the climate models participating to the fifth phase of Coupled Model Intercomparison Project (CMIP5), and two climate warming scenarios, i.e. the Representative Concentration Pathways 2.6 W/m² (RCP2.6) and 8.5 W/m² (RCP8.5). These three models were

CNRM-CM5, IPSL-CM5A-MR and NorESM1-M. CNRM-CM5 is jointly developed by CNRM-GAME and CERFACS in France with a resolution of $1.5^\circ \times 1.5^\circ$ (Voldoire *et al.*, 2013), while IPSL-CM5A-MR has a low resolution of $1.25^\circ \times 2.5^\circ$ (Dufresne *et al.*, 2013). NorESM1-M is built by the virtual Norwegian Climate Centre with a horizontal resolution of approximately $1.9^\circ \times 2.5^\circ$ (Bentsen *et al.*, 2013). Each temperature dataset during 2069-2100 was calibrated by adding the difference between the mean annual temperature (MAT) from WFDEI during 1980-2005 and the MAT from the corresponding CMIP5 models.

2.3 Process-based phenology models

Four process-based spring phenology models were used in this study, including one one-phase model and three two-phase models. The model structures and functions are provided in Table 1. The one-phase model, i.e., the Thermal Time model, only accounts for the ecodormancy phase (Cannell & Smith, 1983). It assumes that the chilling requirement is always fulfilled before the start of forcing accumulation period (often set at January 1st). Leaves then unfold once the accumulated forcing reaches the required critical value F_{crit} (Table 1). The forcing rate for development is a linear function of daily mean temperature, accumulating when daily temperature exceeds the critical temperature T_b (Table 1).

The three two-phase models are the Sequential model (Sarvas, 1974), the Parallel model (Landsberg, 1974) and the Unified model (Chuine, 2000). The main difference between the Sequential model and the Parallel model is in the start of the forcing phase relative to the chilling phase (Table 1). For the Sequential model, the forcing phase begins only after the chilling

requirement is fulfilled, while in the Parallel model chilling and forcing start simultaneously, but the amount of accumulated chilling units influences the forcing accumulation function. The accumulation rate of chilling of both the Sequential and the Parallel model is a triangle function to the optimum temperature between minimum ($T_a = -3.4\text{ }^{\circ}\text{C}$) and maximum temperature ($T_c = 10.4\text{ }^{\circ}\text{C}$) (Chuine, 2000; Sarvas, 1974). Chilling units are accumulated after a given starting date, which was set on 1st September following a previous study (Caffarra *et al.*, 2011b). Forcing units for both these models followed a sigmoid temperature function (Table 1). The leaf unfolding date was defined as the day when the cumulated forcing units reached the required critical value F_{crit} .

The Unified model was developed as a general model for the one-phase and two-phase models, and combines the consecutive sequence of chilling and forcing phases (Chuine, 2000). However, the cost function for its flexible structure contains more parameters than the other models (Table 1), which may result in internal correlation among parameters and in increased uncertainty in model predictions (Fu *et al.*, 2012a). The chilling function of the Unified model is similar to the triangle function of the Sequential and Parallel models. Three parameters are needed: T_1 controls the temperature range during which chilling is accumulated. T_2 determines the maximum of chilling rate when temperature reaches T_3 — the optimum temperature for chilling (Table 1). The rate of forcing is a sigmoid temperature function (Table 1). The Unified model also includes a negative exponential relationship between the state of chilling and the state of forcing, which becomes active after the chilling requirement reaches a critical value.

2.4 Optimization of the phenology models

Because our main aim was to project FLU in a future, warmer world, we first needed to establish which models performed best under current-day warm conditions. We therefore parameterized the models using observations from the 30% warmest winters during 1980-2012 for each site. For each species, we used 80% of the observation site-years in warm winters for model parameterization, and 20% for model evaluation. The particle swarm optimization (PSO) algorithm was applied for parameters estimation (Roberts *et al.*, 2015). The algorithm is based on the social behavior of bird flocks, and aims at searching the minimum value of the root mean square error (internal RMSE) between the predicted and observed phenology. In addition, a new performance criteria DIST between the predicted and observed phenology was also used to fit each phenology model, because it represented both spatial and temporal extremes of leaf unfolding dates across a region (Peaucelle *et al.*, 2019). Firstly, several sets of initial values and ranges for parameters as particle swarm were chosen. Then, each particle adjusted its position in the search space according to its own inertia, the best location it passed by along its path, and the best location the other particles passed by with some random factors. Finally, the particle swarm moved close to the optimum location for the objective function-RMSE in the study (Poli *et al.*, 2007). Then, the external RMSE was calculated with the remaining 20% of the observations and simulations by running the models using parameters derived as described above and temperature data series.

2.5 Map of tree species in Europe

To predict the spatially explicit changes of leaf unfolding date under future climate warming conditions, for each studied species, we used the European tree species distribution map (Brus *et al.*, 2012) with a spatial resolution of 1×1 km, which was based on the National Forest Inventories (<http://www.enfin.info/>). For each pixel, the area percentage of forest was obtained by summing the percentages of all tree species in the pixel. We only considered the pixels where the forest area percentage was more than 25% and the latitude was less than 60° (Fig. A.2). The studied species were *Alnus* spp., *Betula* spp., *Fagus* spp., *Fraxinus* spp. and *Quercus robur* & *Quercus petraea*. Across Europe, *Alnus* spp., *Fagus* spp. and *Fraxinus* spp. are mainly represented by *Alnus glutinosa*, *Fagus sylvatica*, *Fraxinus excelsior*, respectively. As for *Betula* spp. (Fig. A.2), *Betula pendula* occurs more frequently than *Betula pubescens* across *Betula*'s distribution range (Beck *et al.*, 2016). Therefore, we assumed that *Betula pendula* was representative for *Betula* spp. in this study. *Quercus robur* and *Quercus petraea* co-occur at many sites and often produce fertile hybrids (Eaton *et al.*, 2016). Given their similar physiology, we pooled the *Quercus petraea* data with the more abundant *Quercus robur*. Then, FLU of these five tree species were estimated by the four phenology models across their distribution ranges.

3. Results

3.1 Model performance during 1980-2012

For each tree species, parameter estimations are shown in Table A.1. Large differences occurred in the performance of the four models. According to the internal (using calibration data) and external (using only evaluation data) RMSEs, the two-phase models outperformed the one-phase model for *Alnus glutinosa*, *Betula pendula*, *Fagus sylvatica* and *Fraxinus excelsior*, while similar

model performances were obtained for *Quercus robur* (Table 2). And according to DIST, the two-phase models were still better than one-phase model across all tree species (Table A2). These results suggest that the two-phase models are also better suited for future projections. Across all species, when plotted against the observations, the simulated FLU were distributed around the 1:1 line (Fig. 1). More than 75% of year-site combinations exhibited an absolute difference between the observed and the internal simulated FLU less than the internal RMSE for each model, and this did not decline in the external simulation. The number of year-site combinations where the observed FLU was earlier than the simulated FLU was almost equal to that where it was later. The internal and external RMSEs for the four models were around 10-12 days (Fig. 1 a-d), but again, the two-phase models performed better than the one-phase model (smaller RMSE values, i.e. 12 days vs. 10 days for the one- and two- phase models, respectively). The Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC) values also supported the conclusion that the two-phase models performed better than the one-phase model (Table A.3).

In addition, a station-based climate dataset—ECAD was also used to fit each model. Consistent with results based on the gridded climate dataset, across all species, the internal and external RMSEs for the four models were around 11-15 days (Fig. A.3), and the two-phase models performed better than the one-phase model for each species, based on RMSEs, AIC and BIC (Table A.4, Table A.5). Therefore, in the remainder of this study, only results from the two-phase models based on the gridded climate data are presented and discussed. In addition, to test the importance of photoperiod in our analysis, we assumed that latitude was a good proxy photoperiod. Hence, if the models do not exhibit different fits along the latitudinal gradient,

photoperiod would be irrelevant as a driver of FLU. When putting all tree species together, no significant differences in ΔFLU were found along the latitudinal gradient (Fig. A.5), suggesting that photoperiod does not explain additional variation in FLU. However, *Betula pendula* did not follow this overall pattern because in this species latitude did explain differences in ΔFLU in all models (Fig A.4).

3.2 The modeled mean dates of FLU during 1980-2010 across Europe

For each pixel dominated by one of the five study species, we modeled the FLU dates during 1980-2010 using the three two-phase models. Figure 2 (b1-b3) shows the spatial distribution of the mean dates of FLU across Europe from 1980 to 2010 ($\text{MFLU}_{1980-2010}$) for the three two-phase models. Similar spatial patterns of the modeled $\text{MFLU}_{1980-2010}$ were found among these three models. Across the whole of Europe, mean values of $\text{MFLU}_{1980-2010}$ were 127 ± 14 , 128 ± 13 and 127 ± 12 for the Sequential model, Parallel model and Unified model, respectively (Fig. 2 b1-b3).

3.3 Mean end dates of the chilling period during 1980-2010 across Europe

The mean end dates of the chilling period ($\text{MEOC}_{1980-2010}$) were calculated over the period 1980-2010. We found that the mean end dates were substantially different between the Sequential and Parallel model. The $\text{MEOC}_{1980-2010}$ calculated by the Parallel model (Fig. 2 c2) occurred about 1-2 months later than that of the Sequential model (Fig. 2 c1). For the Sequential model, we found that the $\text{MEOC}_{1980-2010}$ was in February to April (Fig. 2 c1). Compared with the other two-phase

models, MEOC₁₉₈₀₋₂₀₁₀ became advanced, and across 79% of the pixels MEOC₁₉₈₀₋₂₀₁₀ occurred in November and December of the previous year for the Unified model (Fig. 2 c3).

3.4 Projected changes in mean dates of FLU (2070-2100 vs 1980-2010, Δ MFLU)

Based on the two-phase models, which all performed equally under current-day conditions, we found that, under the RCP2.6 scenario, MFLU₂₀₇₀₋₂₁₀₀ advanced compared to MFLU₁₉₈₀₋₂₀₁₀ in 75%, 73% and 78% of all pixels for the Sequential, Parallel and Unified models, respectively (Fig. 3 a1). On average across all the pixels, for the three two-phase models MFLU₂₀₇₀₋₂₁₀₀ advanced by 4 days compared to MFLU₁₉₈₀₋₂₀₁₀ (Fig. 3 a1). However, for *Alnus* or *Betula* the mean dates of MFLU₂₀₇₀₋₂₁₀₀ advanced 1-2 weeks compared to MFLU₁₉₈₀₋₂₀₁₀, thus much more than for the other three, later, species (Δ < 7 days) (Fig. 3 a2-a6). In addition, for each tree species advancement of MFLU₂₀₇₀₋₂₁₀₀ were substantially different among the three two-phase models. Especially, for *Fraxinus* and *Quercus* spp the difference of Δ MFLU among the two-phase models was around 5-8 days, larger than other three tree species (3-4 days).

Under the RCP8.5 scenario, the absolute advancements of MFLU₂₀₇₀₋₂₁₀₀ largely exceeded those under RCP2.6 (Fig. 4 a1). Across all pixels, the average advancement of MFLU was 18, 14 and 17 days for the Sequential, Parallel and Unified models, respectively (Fig. 4 a1). For *Alnus* and *Betula*, 3-4 weeks advancement was found, while only 1-2 weeks advances were obtained for the other species (Fig. 4 a2-a6). However, the uncertainty of Δ MFLU among the three two-phase models was still large. For *Fraxinus* and *Quercus* spp, the uncertainty was as large as about two weeks (13-14 days), while for other species, it was about one week (6-7 days).

3.5 Changes in mean end dates of chilling (2070-2100 vs 1980-2010, Δ MEOC)

Under the RCP2.6 scenario, we found that the mean MEOC₂₀₇₀₋₂₁₀₀ for the Sequential and the Parallel model advanced in 84% of the area, while for the Unified model, the mean MEOC was delayed in 89% of the area (Fig. 3 b1). The averages of Δ MEOC were -9 days, -4 days and +7 days (+: delay, -: advance) for the Sequential -, Parallel - and Unified model, respectively (Fig. 3 b1). The mean absolute values of Δ MEOC in *Alnus* and *Betula* (> 7 days) were larger than those of *Fagus*, *Fraxinus* and *Quercus* (< 7 days) (Fig. 3 b2-b6). Similar patterns were found under the RCP8.5 scenario, but the magnitudes of Δ MEOC were much larger than those under the RCP2.6 scenario. In detail, the mean Δ MEOC for the Sequential, Parallel and Unified models were -15, -14 and +19 days, respectively (Fig. 4 b1). Similar to RCP2.6, the mean absolute values of Δ MEOC in *Alnus* and *Betula* (~20 days) were larger than those of *Fagus*, *Fraxinus* and *Quercus* (~10 days) under RCP8.5 (Fig. 4 b2-b6).

3.6 Projected changes in mean dates of FLU relative to changes in mean end dates of chilling (Δ MFLU/ Δ MEOC)

When MEOC was delayed by 1 day, on average across all the pixels, MFLU changed by +0.63 (+0.58), +1.02 (+1.01), -0.71 (-0.98) days under the RCP2.6 (RCP8.5) scenario in the Sequential, Parallel and Unified model, respectively (Fig. 3 c1-c3, Fig. 4 c1-c3). In the Parallel model, under both climate scenarios, Δ MFLU/ Δ MEOC remained confined (> 90% of simulations) within [0.8-1.2] across the species distribution ranges (Fig. 3 c2, Fig. 4 c2). In contrast, high spatial heterogeneity in Δ MFLU/ Δ MEOC occurred in the simulations with the Sequential and Unified model. Results obtained with the Sequential model yielded smaller

delays in FLU per day delay in MEOC than results obtained with the Parallel model, with $\Delta \text{MFLU} / \Delta \text{MEOC}$ values above 1 occurring in only 28% of the pixels under the RCP2.6 scenario, and 34% under the RCP8.5 scenario (Fig. 3 c1, Fig. 4 c1). In contrast to the Parallel and Sequential models, in the Unified model MFLU generally advanced when MEOC delayed by 1 day, with 34% of the pixels exhibiting $\Delta \text{MFLU} / \Delta \text{MEOC}$ less than -1 (advances by more than one day per day delay in MEOC) under the RCP2.6 scenario, increasing to 56% of the pixels under the RCP8.5 scenario (Fig. 3 c3, Fig. 4 c3).

4. Discussion

4.1 Model performance

Previous model comparison studies have been inconclusive regarding which phenology model best simulates FLU dates. Some studies have suggested that the one-phase model, which only considers the ecodormancy phase, performed better than two-phase models, which consider both the endodormancy and ecodormancy phases (e.g. Fu *et al.*, 2012b; Linkosalo *et al.*, 2008). These studies suggested that chilling accumulation always sufficed to break endodormancy and therefore that the chilling status did not need to be considered in the phenology models. Other studies have found similar performance between one-phase and two-phase models, but suggested that the two-phase models are more appropriate for the prediction of leaf unfolding dates, especially under future climate warming conditions when the chilling requirement might become insufficient (e.g. Basler, 2016; Vitasse *et al.*, 2011). Our study found that the two-phase models performed slightly better than the one-phase model under current-day warm conditions. This difference may be attributable to the recent occurrence of warm autumns and winters, with

insufficient chilling increasingly affecting the trees' leaf unfolding dates (Cook *et al.*, 2012). Therefore, the models including a chilling period performed better in this study.

Under global warming the two-phase models that explicitly consider the chilling effect can be considered conceptually better than the one-phase model to predict future changes in leaf unfolding (Legave *et al.*, 2008; Vitasse *et al.*, 2011). Climate warming in autumn and winter slows the rate of chilling accumulation. As autumn and winter temperatures continue to increase, accounting for the impacts of chilling on leaf unfolding may increase in importance, because insufficient chilling could attenuate or even reverse the advancement of spring phenology (Cook *et al.*, 2012; Guo *et al.*, 2015; Morin *et al.*, 2009). In addition, the local acclimation is important for phenology model calibration, since the effect size of warming could vary along with the interacting factor (e.g., chilling or photoperiod) when applying the models across a larger region (Montgomery *et al.*, 2020; Peaucelle *et al.*, 2019). Therefore, the local acclimation in key parameters, such as growing degree days, should be investigated to improve the model performance (Chuine & Régnier, 2017; Fu *et al.*, 2014b; Peaucelle *et al.*, 2019; Rea & Eccel, 2006).

Almost all spring phenology modules used in Land Surface models rely solely on temperature to simulate the date of leaf unfolding in spring. However, several studies have already convincingly shown that budburst phenology is also affected by other environmental factors, such as precipitation (Fu *et al.*, 2014b), air humidity (Laube *et al.*, 2014b) and photoperiod (Basler & Körner, 2014; Caffarra & Donnelly, 2011a; Fu *et al.*, 2019). Among these factors, especially the

photoperiod effects have been widely discussed. Photoperiod provides a more stable signal than temperature, and may help trees reducing frost risks under warmer climates (Bennie *et al.*, 2010; Way & Montgomery, 2015) and help avoiding too late leaf unfolding (Caffarra & Donnelly, 2011a; Pletsers *et al.*, 2015; Fu *et al.*, 2019). However, the photoperiod effect is species-specific and more prominent in warm-temperate than in northern climates (Heide, 1993; Laube *et al.*, 2014a; Zohner *et al.*, 2016). In our analysis, we did not find significant differences along the latitudinal gradient. It might be caused by averaging species at the regional level and low resolution climate datasets (Olsson & Jönsson, 2015). Therefore, the possible photoperiod effect could not be excluded at the species level.

4.2 Differences in Δ MFLU among the two-phase models

The patterns of modeled leaf unfolding dates (MFLU) during 1980-2010 in our study were consistent with spring phenology patterns based on remote sensing or processed-models in other studies (Bennie *et al.*, 2010; Fu *et al.*, 2014a; Wang *et al.*, 2015). We further found, across the three two-phase models, that the MFLU₂₀₇₀₋₂₁₀₀ advanced about one week and three weeks compared to MFLU₁₉₈₀₋₂₀₁₀ under the RCP2.6 and RCP8.5 scenarios, although the amplitude was species-specific. The early unfolding species *Alnus* and *Betula* advanced more than the other three species. This confirms that pioneer species are more sensitive to climate warming than late successional species, which is in line with results from former studies (Menzel *et al.*, 2006b; Morin *et al.*, 2009). However, our results also highlight that this difference between early- and late successional species also remains under severe warming in the RCP 8.5 scenario.

Interestingly, we found that the projected leaf unfolding dates differed substantially among the three two-phase models. What's more, the mean difference of ΔMFLU was as large as around 14 days for *Fraxinus* spp. The divergent of the projected leaf unfolding dates would result in over or under-estimation of annual productivity by 13% (Richardson *et al.*, 2011). In addition, it increased the uncertainty in spring or summer soil moisture and summer heatwaves (Lian *et al.*, 2020). However, these phenology models were still widely embedded in land surface models currently ((Kucharik, 2003; Sitch *et al.*, 2003; Thornton *et al.*, 2002), in which the phenology was triggered when accumulated growing degree days (GDD) exceeds a threshold GDD_{crit} . Therefore, it is crucial to improve the accuracy of phenology models for the sake of accurate projections of ecosystem gross productivity, which needs the accurate spring phenology determining growing season length, and climate changes, which require the accurate assessment of vegetation feedbacks.

The divergent of the projected leaf unfolding dates must be related to the different assumptions regarding the impact of changes in the end dates of chilling (ΔMEOC) and in the associated chilling period. Recent studies have suggested that phenology models calibrated not only by observed leaf unfolding dates, but also by endodormancy break dates could improve the performance of phenology models (Chuine *et al.*, 2016). However, the dynamics of the chilling period have been studied only rarely. Experimental results from Western European fruit trees suggested that the endodormancy break likely occurs between December and February (Chuine *et al.*, 2016; Legave *et al.*, 2013), which is consistent with our results from the Sequential and the Unified model. In contrast, the end dates of the chilling period in the Parallel model either were the date when endodormancy broke, or in case of incomplete chilling during very warm winters,

that date when leaves unfolded. Thus, the patterns of MEOC₁₉₈₀₋₂₀₁₀ varied a lot among the three two-phase models. Without addressing the lack of understanding of the interactions between the endodormancy and the ecodormancy phases, this uncertainty will continue to exist. Experimentally determining exactly when the endodormancy breaks and how this affects spring phenology is thus a priority for making progress in predicting spring phenology changes in a future world (Chuine *et al.*, 2016; Junttila & Hänninen, 2012; Leinonen, 1996).

4.3 Opportunities for better calibration of EOC

Current representation of chilling leads to overestimation of the advanced spring phenology by about 1-3 weeks (Wang *et al.*, 2020). Therefore, a better interpretation of chilling and thus a better calibration of MEOC is indeed necessary to improve the spring phenology models. First, the start of the period during which buds accumulate chilling, the endodormancy phase, remains uncertain. In temperate tree species, the starting date of the chilling period is usually defined as a fixed date between September and November (Cannell & Smith, 1983; Landsberg, 1974), but these choices are based on little evidence. Second, the chilling accumulation at different cold temperatures also remains highly uncertain. Chilling was assumed to exert maximum effect between 0°C and 5°C (Cannell & Smith, 1983; Landsberg, 1974), but the effect of freezing temperature should not be ignored (Wang *et al.*, 2020), rendering the effectiveness of freezing temperature for chilling remain to be explored. In addition, day and night temperature might exert different effects on the accumulation of chilling, given their different effects on spring phenology (Fu *et al.*, 2016; Piao *et al.*, 2015). Third, alternation of cold and warm days during endodormancy may be less effective for chilling accumulation than the same number of cold days in a continuous cold spell (Bailey & Harrington, 2006). Similarly, a warm spell during

endodormancy is typically ignored when accumulating warm temperatures, but this is not certain (Bailey & Harrington, 2006). Future research should aim at elaborating these unknowns regarding chilling accumulation.

4.4 The importance of changes in chilling to leaf unfolding dates

We evaluated the importance of changes in chilling relative to forcing in determining leaf unfolding dates, and determined to what extent Δ MEOC and changes in forcing period impacted on Δ MFLU. For the Sequential and the Parallel model, the advancements of MFLU could mainly be attributed to the advancements of MEOC. In contrast, for the Unified model, the advancement of MFLU was mainly attributable to the shortened forcing period. This difference is caused by the different representation of the chilling mechanism in the two-phase models, especially their different optimum temperatures for chilling accumulation. In our study region, mean winter temperature is projected to rise from around 3 °C (the optimum temperature for chilling in the Unified model) during 1980-2010 to around 5 °C (the optimum temperature for chilling in the Sequential model) during 2070-2100. Therefore, chilling accumulates increasingly faster in the Sequential model when going from the current climate to the future climate, while in the Unified model chilling accumulates increasingly slower. For the parallel model, the best fitting optimum temperature for chilling was generally below 0 °C, so the accumulation of chilling was typically too small to fulfill the chilling requirement. Therefore, in about 80% of the cases, chilling was not completely fulfilled in our simulations with the parallel model, which became even more frequent in a future, warmer climate.

5. Conclusions

Our analysis has demonstrated that the two-phase phenology models perform slightly better than the one-phase model under current-day conditions. However, although all three two-phase models simulated advanced leaf unfolding in the period 2070-2100, projected leaf unfolding dates differed substantially among the two-phase models over the period 2070-2100, which was related to the different model assumptions regarding both chilling and forcing periods. We found that the modeled end dates of the chilling period advanced in both the Sequential and Parallel models during the period 2070-2100 compared to the period 1980-2010, but delayed in the Unified model. These findings reveal large uncertainty regarding the mechanism underlying the leaf unfolding process in the two-phase phenology models. We therefore claim an urgent need to improve our understanding of the leaf unfolding process in order to improve the representation of phenology in the terrestrial ecosystems in future.

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Fig. 1 Relationship between observed dates of spring first leaf unfolding and dates simulated with four different phenology models: Thermal Time model (a and e); Sequential model (b and f); Parallel model (c and g); and Unified model (d and h). Data are shown for all years and species included in our analysis (see Methods section). The upper panels show the relationship between the model simulations and the data used to fit the model (internal simulations; a-d). The lower panels show the relationship between the model simulations and independent data that were not used to fit the model (external simulations; e-h). Colors indicate the numbers of occurrence. The black line in each figure is the 1:1 line. The numbers in the lower right corner indicate the root mean square error (RMSE).

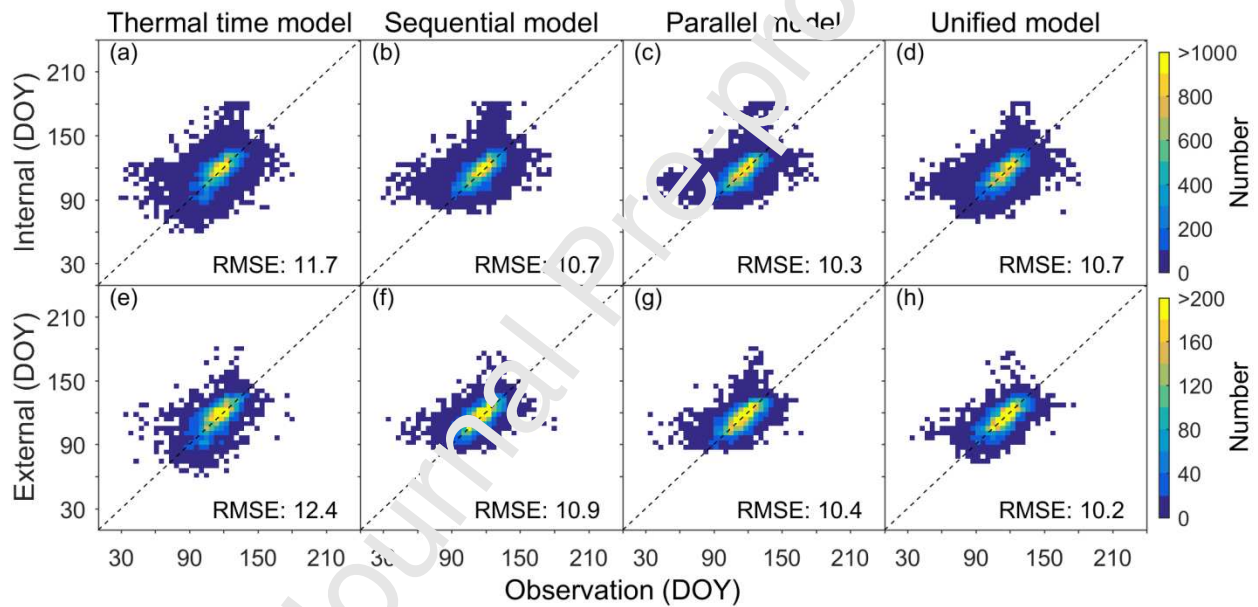


Fig. 2 Spatial distributions of the observed mean dates of first leaf unfolding (MFLU, a1-a6) and the simulated MFLU and the mean end dates of the chilling period (MEOC) during the period 1980-2010 for the Sequential model (b1, c1), Parallel model (b2, c2) and Unified model (b3, c3).

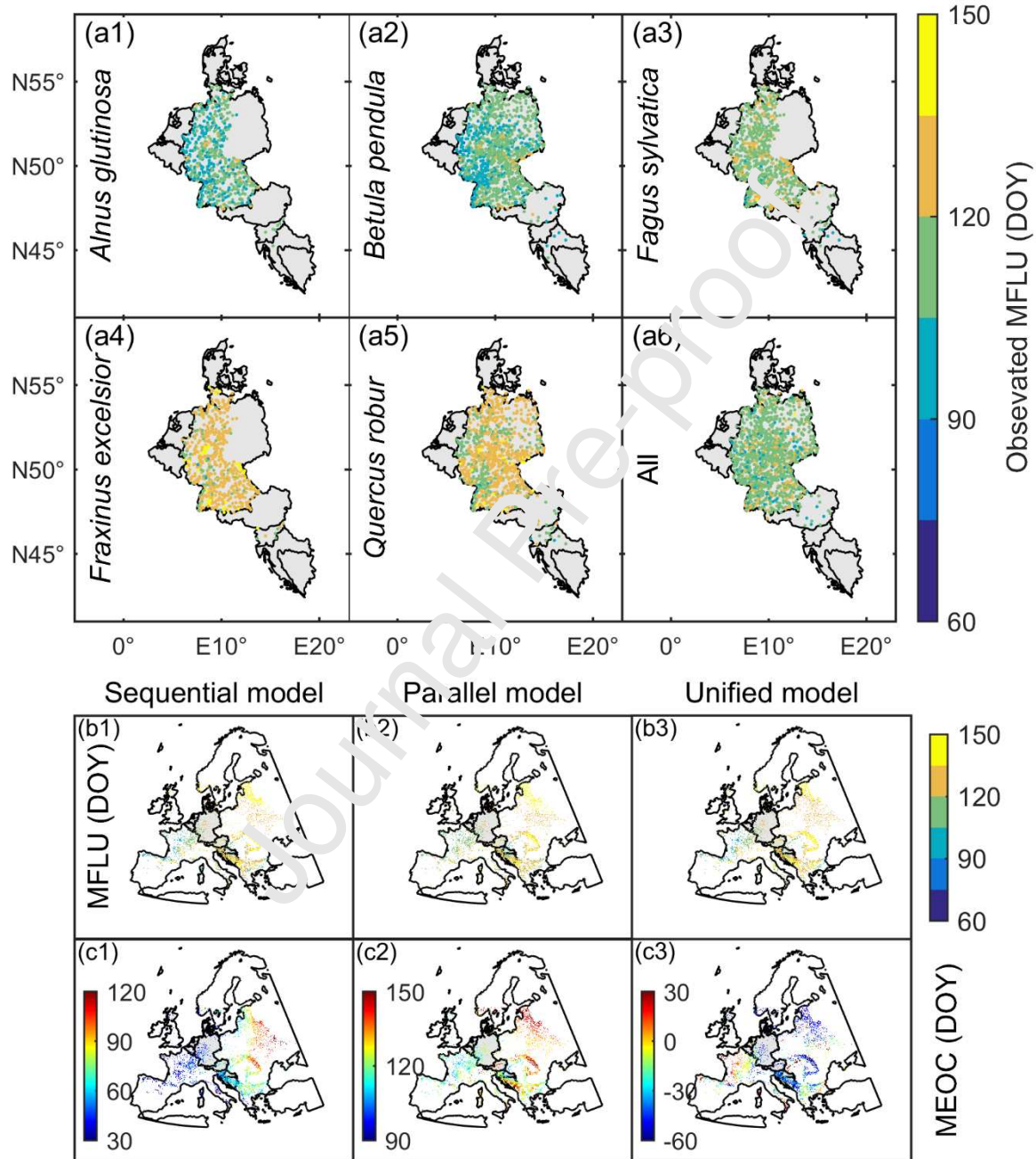


Fig. 3 Histograms of the changes in mean unfolding dates (Δ MFLU, a2-a6) and end dates of chilling periods (Δ MEOC, b2-b6) for the five study species under the RCP2.6 scenario, relative to the current period 1980-2010 and the spatial patterns of Δ MEOC/ Δ MFLU (c1-c3). Two subfigures (a1, b1) in the top left corner show the histograms of all tree species combined. QR & QP: *Quercus robur* & *Quercus petraea*. The numbers in parentheses indicate the mean of Δ MFLU and numbers in brackets indicate the standard deviation of Δ MFLU.

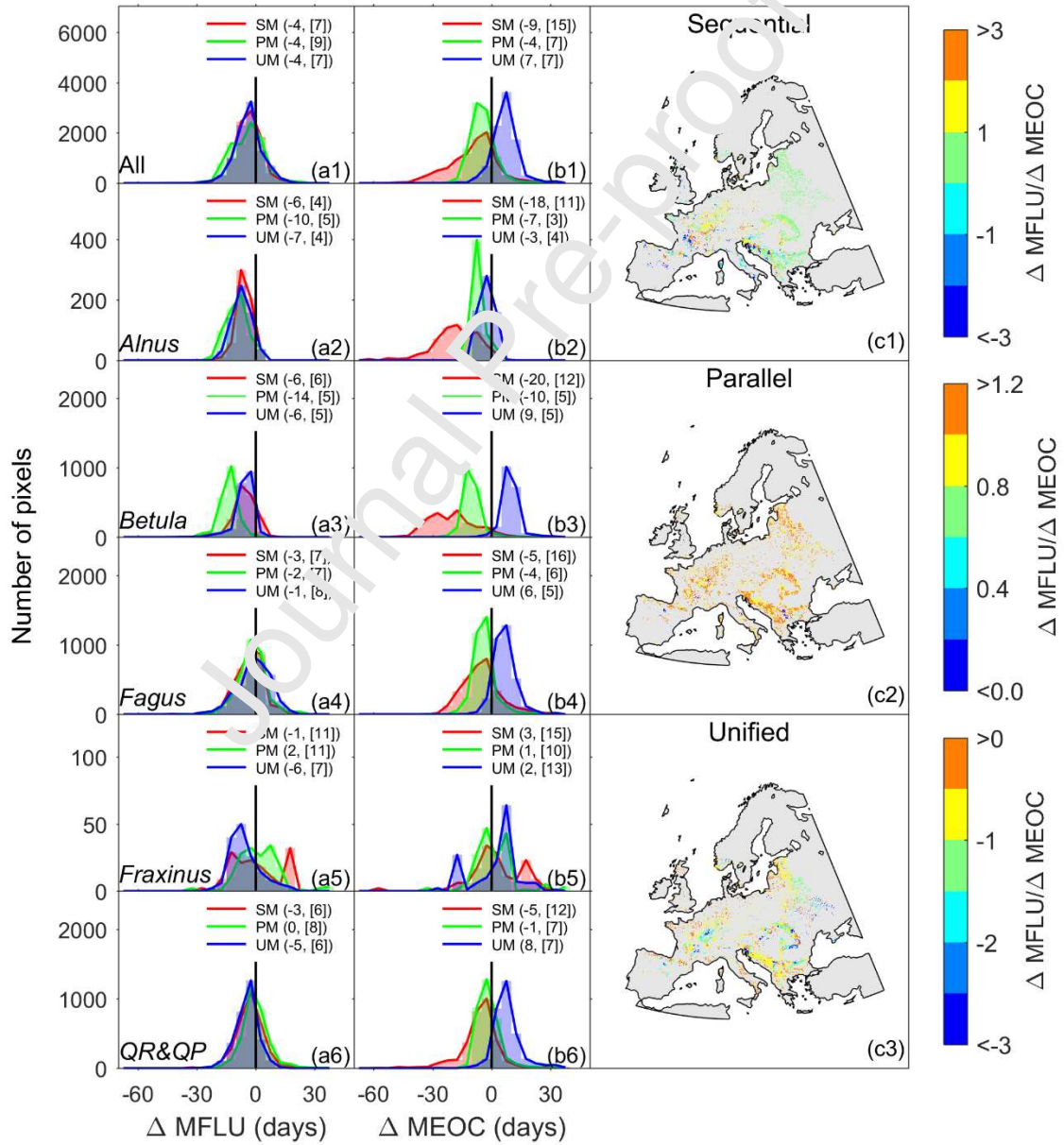


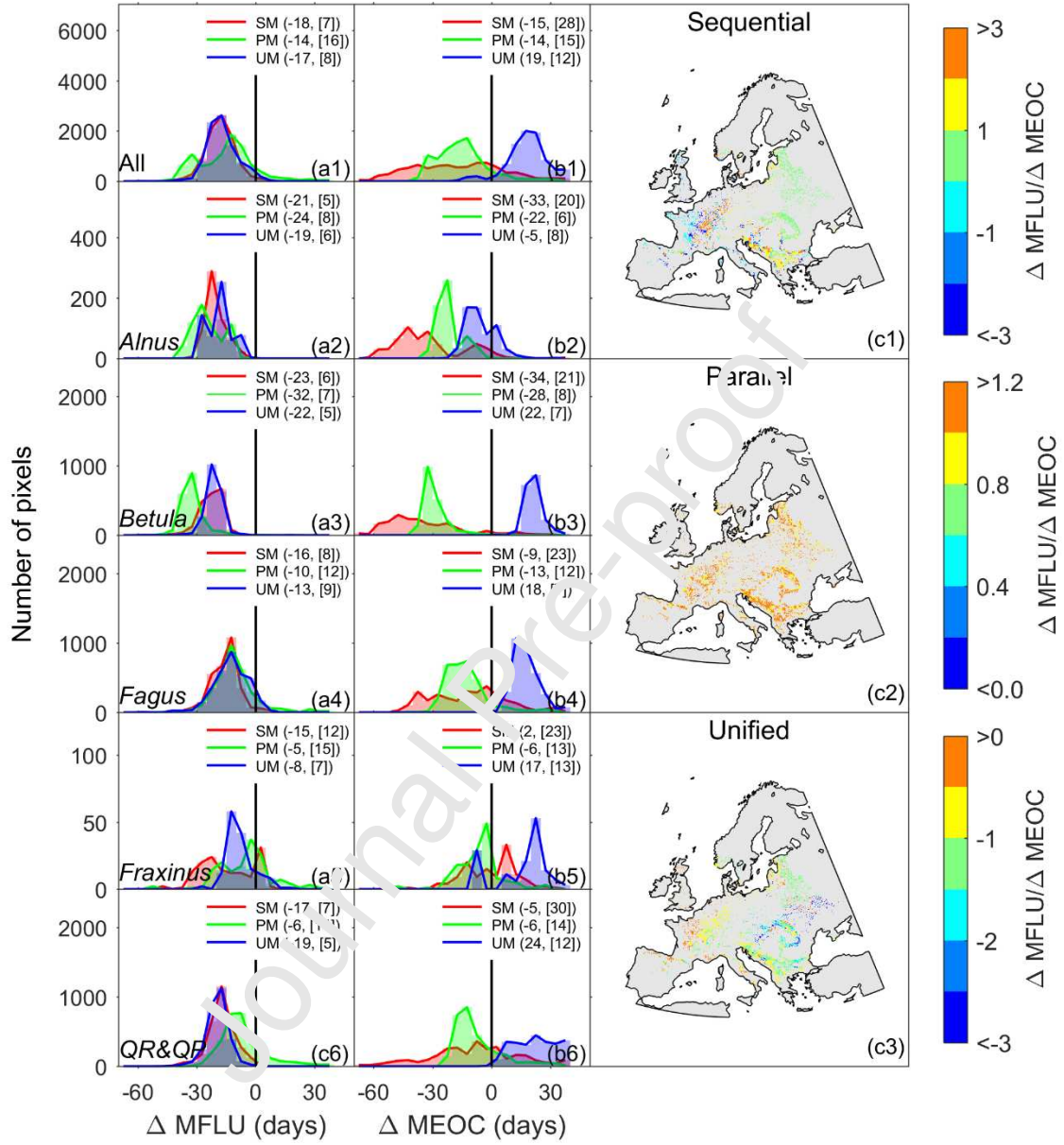
Fig. 4 Similar to Fig. 3, but under the RCP8.5 scenario.

Table 1 Temperature response functions and structures of the four phenology models used in this study. i , j : the day of year. t_f : the starting day of the forcing period. t_c : 1st September. T_i : mean temperature on i^{th} day of year. R_{ci} : rate of chilling on i^{th} of year. R_{fi} : rate of forcing on i^{th} day of year. T_a and T_c are the minimum and maximum temperature for chilling. $T_a = -3.4$ °C, $T_c = 10.4$. Bold characters indicate to be fitted. TM: Thermal Time model; SM: Sequential model; PM: Parallel model; UM: Unified model.

	Temperature response function		Structure	Number of parameters
	Chilling period	Forcing period		
T M		$R_{fi} = \begin{cases} 0, & T_i \leq T_b \\ T_i - T_b, & T_i > T_b \end{cases}$	$F_{crit} = \sum_{i=t_f}^{sos} R_{fi}$ (t_f : 1st, January)	2
S M	$R_{ci} = \begin{cases} 0, & T_i \leq T_a \\ \frac{T_i - T_a}{T_b - T_a}, & T_a < T_i \leq T_b \\ \frac{T_i - T_c}{T_b - T_c}, & T_b < T_i < T_c \\ 0, & T_i \geq T_c \end{cases}$	$S_{cj} = \sum_{i=t_c}^j R_{ci}$ $K_j = \begin{cases} 1, & S_{cj} \geq C_{crit} \\ 0, & S_{cj} < C_{crit} \end{cases}$ $R_{fi} = \begin{cases} 0, & T_i \leq T_d \\ \frac{1}{K_i \left(1 + e^{\alpha(T_i + \beta)} \right)}, & T_i > T_d \end{cases}$	$C_{crit} = \sum_{i=t_c}^{t_f-1} R_{ci}$ $F_{crit} = \sum_{i=t_f}^{sos} R_{fi}$	6
P M	$R_{ci} = \begin{cases} 0, & T_i \leq T_a \\ \frac{T_i - T_a}{T_b - T_a}, & T_a < T_i \leq T_b \\ \frac{T_i - T_c}{T_b - T_c}, & T_b < T_i < T_c \\ 0, & T_i \geq T_c \end{cases}$	$S_{cj} = \sum_{i=t_c}^j R_{ci}$ $K_j = \begin{cases} K_{min} + \frac{1 - K_{min}}{C_{crit}} S_{cj}, & (S_{cj} < C_{crit}) \\ 1, & (S_{cj} \geq C_{crit}) \end{cases}$ $R_{fi} = \begin{cases} 0, & T_i \leq T_d \\ \frac{1}{K_i \left(1 + e^{\alpha(T_i + \beta)} \right)}, & T_i > T_d \end{cases}$	$C_{crit} = \sum_{i=t_c}^{t_{cend}} R_{ci}$ $F_{crit} = \sum_{i=t_c}^{sos} R_{fi}$	7
U M	$R_{ci} = \frac{1}{1 + e^{T_1(T_i - T_3)^2 + T_2}}$	$R_{fi} = \frac{1}{1 + e^{\alpha(T_i - \beta)}}$	$C_{crit} = \sum_{i=t_c}^{t_f-1} R_{ci}$ $we^{zS_{cj}} = \sum_{i=t_f}^{sos} R_{fi}$ $S_{cj} = \sum_{i=t_c}^j R_{ci}$ ($j = t_f + 1, \dots, t_{tot}$)	9

Table 2 Internal RMSE shows the root mean square error between observed dates of spring first leaf unfolding used to fit the model and the model simulations with four different phenology models for each tree species. External RMSE shows the root mean square error between independent observed data that were not used to fit the model and the model simulations. TM: Thermal Time model; SM: Sequential model; PM: Parallel model; UM: Unified model.

Phenological model/			<i>Alnus</i>	<i>Betula</i>	<i>Fagus</i>	<i>Fraxinus</i>	<i>Quercus</i>	
Tree Species			<i>glutinosa</i>	<i>pendula</i>	<i>sylvatica</i>	<i>excelsior</i>	<i>robur</i>	
RMSE (day's)	One-phase	TM	Internal	15.7	11.1	12.2	10.3	9.9
			External	15.8	12.2	13.8	15.7	9.7
	Two-phase	SM	Internal	14.1	9.8	10.1	10.3	10
			External	14.7	10.1	8.6	9.6	11.6
		PM	Internal	13.8	9.7	9.3	9.8	9.3
			External	14.2	9.5	9.6	9.7	9.8
		UM	Internal	13.8	10.1	10	10	10
			External	13.5	9.7	9.6	10.8	8.6

AuthorCredit Statement

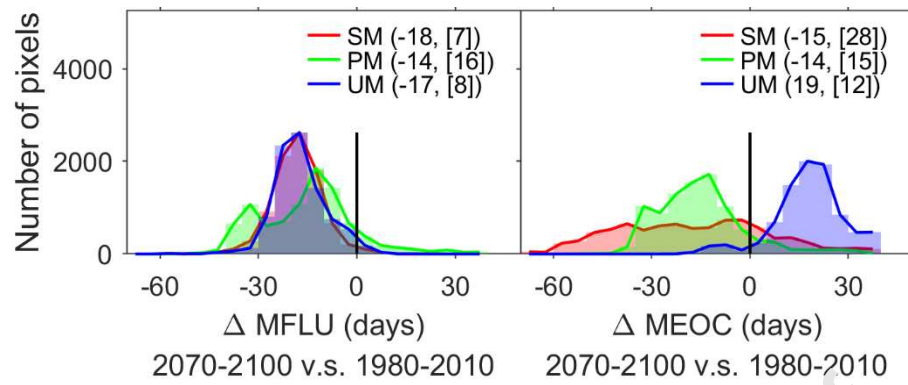
H. Z. and X. W. designed the research; H. Z. performed the analyses; H. Z., Y. F. and X. W. drafted the paper; all authors contributed substantially to interpretation of the results and revision of the texts.

Journal Pre-proof

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Graphical abstract

Highlights:

- When fitting to the observed dates in warm winter, two-phase phenology models performed slightly better than the one-phase model.
- The projected leaf unfolding dates advanced but diverged substantially among the two-phase models over the period 2070-2100.
- The end dates of chilling period advanced in the Sequential model and Parallel model during 2070-2100 compared to 1980-2010, but delayed in the Unified model.