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1 1 **Bayesian comparison of six different temperature-based**
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4 2 **budburst models for four temperate tree species**
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1 10 **Abstract**

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3 11 Phenology models are tools to analyze changes in the timing and duration of the
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6 12 growing season. During the past three decades different budburst models have been
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9 13 developed, but, so far, no consensus model has been found to accurately predict
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12 14 budburst date across different tree species. The aim of this study was to estimate the
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14 15 performance of six different temperature-driven models of leaf budburst (thermal time,
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16 16 thermal period fixed, sequential, parallel, alternating, unified) for four temperate tree
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18 17 species in Belgium (birch, chestnut, oak, beech). The models were parameterized
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20 18 using a Bayesian approach. The performance of these models was compared using
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22 19 Bayesian model Comparison (BMC) and Root Mean Square Error (RMSE).
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24 20 Model comparison showed that the two models that do not include a calculation of
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26 21 chilling requirement were the best for the studied four tree species. The sequential
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28 22 model (SM) was the third most plausible model for predicting budburst, having a
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30 23 higher probability to be correct than the other two-phase models combining a chilling
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32 24 phase with a forcing phase. This suggested that in our budburst observation dataset,
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34 25 the chilling requirement was probably always fulfilled, making the date of budburst
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36 26 controlled by forcing temperature. We cannot rule out that in warmer regions or future
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38 27 warmer conditions, chilling may become insufficient and a sequential pattern of
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40 28 chilling and forcing may become most appropriate to simulate budburst date.
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42 29 Parameter analysis showed that the last month prior to budburst had the greatest
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44 30 impact on determining the date of bud opening in the case of birch and chestnut,
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46 31 whereas the last three months were the main determinants for oak and beech, the two
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1 32 later flushing species. Validation showed that the models that fitted the
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3 33 parameterization data well had much poorer performance when tested with
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6 34 independent data. This indicates that other factors (e.g. photoperiod) might affect the
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9 35 budburst process and/or model parameterization (determining the sensitivity of
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12 36 budburst to temperature) substantially change between different localities.
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18 37 **Keywords:** Temperate deciduous forest species; Phenology model; Bayesian model
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1. Introduction

The timing of tree budburst is a critical phenological event that controls the dynamics of carbon and water cycling, and establishes a trade-off between capacity adaptation, i.e. maximum use of the growth resources of the site, and survival adaptation, i.e. avoidance of damage caused by late frosts (Heide, 1985; Hänninen and Hari, 1996; Saxe et al., 2001; Leinonen and Hanninen, 2002). Variation in timing of budburst among species can be attributed to different combinations of these adaptive forces.

The traditional explanation of phenological inter-species variation lies in the differences in vulnerability to xylem dysfunctions and to damage by late-frosts by late frosts to leaves (Tyree and Zimmermann, 1983; Wang et al., 1992). However, the mechanism behind bud development is still unclear and the physiological control of the early stages of bud development remains poorly understood. Therefore, only semi-empirical modeling methods have been used to predict the timing of budburst and explore phenological variation among species.

Since Réaumur suggested that differences in daily temperature could be used to explain differences in timing of phenological events (Réaumur, 1935), many different kinds of phenology models based on temperature have been developed. The most simple models, such as the ‘Thermal Time model’, only involve a forcing temperature (Cannell and Smith, 1983). While most of other models distinguish two phase: dormancy and quiescence (Sarvas, 1974; Lavender, 1981; Cannell and Smith, 1983; Murray et al., 1989). First, chilling temperatures (e.g. between -5 to +10°C) are used to determine the date of which bud dormancy break, whereas afterwards forcing

1 61 temperature (e.g. above 0°C) is assumed to induce budburst. Examples of the
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3 62 two-phase models are the ‘Parallel model’ (Landsberg, 1974; Hänninen, 1990; Kramer,
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6 63 1994), the ‘Sequential model’ (Sarvas, 1974; Hänninen, 1987; Kramer, 1994), the
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9 64 ‘Alternating model’ (Cannell and Smith, 1983; Murray et al., 1989; Kramer, 1994);
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12 65 and the ‘Unified model’ (Chuine, 2000). To date no consensus model has been
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15 66 accepted, likely because no model accurately predicts budburst date for different
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18 67 species under all conditions. Most models were developed for single species (*Pinus*
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20 68 *palustris* Mill. (Boyer, 1973); *Picea sitchensis* (Bong.) Car. (Cannell and Smith, 1983);
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23 69 *Fagus sylvatica* L. (Kramer, 1994), and rarely for several species (Hunter and
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26 70 Lechowicz, 1992; Chuine, 2000). Thus, these models are unlikely to reflect the
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29 71 different responses of different species to chilling and forcing temperatures. Another
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32 72 reason for the missing consensus in phenology models may lie in the inadequate
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35 73 mathematical analyses conducted and inadequate criteria employed in evaluating the
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38 74 models (Tuomi et al., 2008). Commonly applied goodness-of-fit criteria, such as the r^2
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41 75 value or the squared sum of residuals (Kramer, 1994; Chuine et al., 1998; Linkosalo et
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44 76 al., 2008; Vitasse et al., 2011) do not account for the uncertainty of the estimates
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47 77 produced by these models.

48 78 In this study, our purpose was to estimate the performance of different models
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51 79 predicting the timing of budburst for four temperate tree species (*Betula verrucosa*
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53 80 Ehrn. (Birch), *Aesculus hippocastanum* L. (Chestnut), *Fagus sylvatica* L. (beech) and
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56 81 *Quercus robur* L. oak) with different time of budburst. We tested six models: the
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59 82 Thermal time model (TTM), the Thermal period fixed model (TPFM), the Sequential

1 83 model (SM), the Parallel model (PM), the Alternating model (AM) and the Unified
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3 84 model (UM). The parameter vectors of the models were calibrated by Bayesian
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6 85 methods (BC), and the best parameter vector for each model was identified by
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9 86 Markov chain Monte Carlo (MCMC) sampling of parameter spaces. BC can exploit a
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11 87 *priori* available statistical information on unknown parameters, thereby significantly
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14 88 improving the precision of parameter estimation (Cobelli et al., 2000; Van Oijen et al.,
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17 89 2005). Model performance was evaluated by using the traditional Root Mean Square
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20 90 Error (RMSE), and Bayesian model comparison (BMC). BMC examines the different
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23 91 models to quantify their relative probabilities of having the correct structure (Kass and
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26 92 Raftery, 1995; Van Oijen, 2008). In addition to the model evaluation, we also tested
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29 93 the influence of different temperature–dependent functions on model performance.
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31 94 Specifically we explored:
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34 95 1. What the relative importance of chilling and forcing temperature is among models.
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37 96 2. Whether different species have similar control mechanisms to drive their budburst
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40 97 phenology, i.e. can one simple model be applied to all species, with different timing of
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43 98 flushing or successional strategy?
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46 99 3. If the estimation of model performance varies when evaluated with different
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48 100 methods i.e. RMSE vs. BMC.

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2. Materials and methods

2.1 Phenology and air temperature data

Budburst records were obtained from six sites of the Observation Network of the Belgian Royal Meteorological Institute (RMI), which collected information on phenological phases of trees and plants in Belgium between the early 1940s and late 1990s. However, in this study we used only the data since 1958 due to the lack of accurate temperature estimations before then. In the RMI phenological dataset the day of bud break corresponded to a visible outcome of the top of the leaves and their contact with the atmosphere for one third of the buds on the tree.

The four species were grouped into two categories i.e. *Betula verrucosa* Ehrn. and *Aesculus hippocastanum* L. with budburst around mid April, *Fagus sylvatica* L. and *Quercus robur* L. with budburst in early May, Table1). These two categories are indicated as ‘early flushing’ and ‘late flushing’. However, this classification goes beyond the date of budburst. In fact, the two late flushing species are late successional species showing one or two leaf growth flush per year, whereas the two earlier flushing species are earlier successional species with continuous leaf growth or multiple leaf flushes. The investigated species are common in Belgium(Matteo Campioli et al., 2012).The details of the sites are shown in Table 2. Values of air temperature for each site (three-hourly averages) were obtained from RMI weather stations nearby the sites.

The number of budburst observations for some species at some sites was too limited to calibrate parameter rich models. Only the site with the highest number of

1 124 observations was used to estimate the model parameters. The pooled dataset from
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3 125 other sites was used as independent dataset to test the models (Table1). We preferred
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6 126 this way to the reverse (i.e. use the pooled dataset for calibration and one site as
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9 127 independent dataset for testing) as it is more consistent to calibrate the models with
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11 128 budburst series collected at one site (thus by the same operator on the same genetic
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14 129 pool) than with less compatible datasets from multiple sites.
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17 130 **2.2 Models for the timing of budburst**

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20 131 We used six models, which can be divided into two general types. The first type
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23 132 (thermal time or growing degree days model, one-phase models) represents the
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26 133 simplest modeling approach to simulate budburst. Accordingly, budburst is triggered
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29 134 when the buds have undergone a sufficient warming (defined as forcing temperature)
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32 135 that cumulated from a fixed date or for a fixed period . In this approach, the dormancy
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35 136 phase is not accounted for, as the environmental conditions required to release
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38 137 dormancy are supposed to have been met before the fixed starting date. The other type
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41 138 of models (two-phase models) considers not only the forcing temperature but also the
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44 139 effect of chilling temperature in breaking the bud's dormancy. Accordingly, both cold
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47 140 and warm conditions control the budburst. A short description of the six models
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50 141 employed (2 of the one-phase and 4 of the two-phase) is given below, whereas their
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53 142 schematic representation is in Fig.1 and their parameters in Appendices A and B. In
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56 143 the description below, next to the name of each model, a reference is made to relevant
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59 144 studies employing the model.

60 145 In the models, the effect of the forcing temperature and of the chilling temperature is

146 accounted for by calculating (daily) rate of forcing (R_f) and of chilling (R_c), that are
 147 functions of the daily air temperature (T). These functions differ between models. R_f
 148 and R_c determine the rates of change of the state of forcing (S_f) and chilling (S_c),
 149 respectively:

$$150 \quad S_f(D) = \sum_{t=t_{1f}}^D R_f(T) \quad (1)$$

$$151 \quad S_c(D) = \sum_{t=t_{1c}}^D R_c(T) \quad (2)$$

152 where t_{1f} and t_{1c} is the initial day of the forcing- and chilling period, respectively, and
 153 D is the day of the year. Budburst is triggered when S_f reaches a forcing threshold F^* ,
 154 whereas, in the models that account for the chilling temperature, the start of
 155 quiescence (the forcing period) is triggered when S_c reaches the chilling threshold C^* .

$$156 \quad \text{if } S_f(D) \geq F^* \quad \text{then Budburst induction completed} \quad (3)$$

$$157 \quad \text{if } S_c(D) \geq C^* \quad \text{then Dormancy completed} \quad (4)$$

158 **2.2.1 Thermal time model (TTM)**(Cannell and Smith, 1983) .

159 In the *TTM*, the forcing period starts on a fixed day ($t_{1f} = t_0$), and R_f is computed only
 160 when the air temperature is above a critical temperature (T_b):

$$161 \quad R_f(D) = \begin{cases} 0 & \text{if } T(D) \leq T_b \text{ or } D < t_0 \\ T - T_b & \text{if } T(D) > T_b \text{ and } D \geq t_0 \end{cases} \quad (5)$$

162 To test for the importance of the formulation of the rate function R_f , a second version
 163 of *TTM* (named *TTM**) was employed. Previous phenological modeling studies have
 164 found that the rates of forcing are either growing degree-days as Eq.5, or sigmoid
 165 functions of the temperature . Therefore in *TTM** we used the forcing rate function as:

$$R_f(D) = \begin{cases} 0 & \text{if } D < t_0 \\ \frac{a}{1 + e^{-b(T-c)}} & \text{if } D \geq t_0 \end{cases} \quad (6)$$

where a, b and c are constants. Overall, in TTM, we have 3 parameters (t_0, T_b, F^*), and 5 parameters for TTM* (t_0, a, b, c, F^*).

2.2.2 Thermal period fixed model (TPFM) (Nizinski and Saugier, 1988).

TPFM is similar to TTM, but in TPFM the forcing temperature is computed and accumulated over a fixed period of N days after the start date t_0 . The start was fixed on the February 1 when the air temperature is normally above the critical temperature T_b , i.e. 0°C. If at the end of such period S_f is greater than the forcing threshold F^* , budburst is initiated, otherwise the start date of the N-day accumulation period moves one day forward. In TPFM, we have 2 parameters (N, F^*)

$$R_f(D) = \begin{cases} 0 & \text{if } D < t_0 \text{ or } T < T_b \\ T - T_b & \text{if } D \geq t_0 \text{ and } T \geq T_b \end{cases} \quad (7)$$

2.2.3 Sequential model (SM). (Sarvas, 1974; Hänninen, 1990; Kramer, 1994).

The SM is similar to the thermal time models in simulating the forcing temperature and the budburst trigger. However, instead of starting the forcing period on a certain date, the SM starts to accumulate warmth units when a sufficient amount of chilling has occurred (Eq. 4). In SM, we fixed t_{lc} on November 1. As in the previous applications of SM, we define R_c as a triangular function of T (Hänninen, 1990; Kramer, 1994)

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$$R_c(D) = \begin{cases} 0 & \text{if } T(D) \leq T_{\min} \\ \frac{T - T_{\min}}{T_{\text{opt}} - T_{\min}} & \text{if } T_{\min} < T(D) \leq T_{\text{opt}} \\ \frac{T - T_{\max}}{T_{\text{opt}} - T_{\max}} & \text{if } T_{\text{opt}} < T(D) \leq T_{\max} \\ 0 & \text{if } T \geq (D)T_{\max} \end{cases} \quad (8)$$

184 where T_{\min} , T_{\max} , T_{opt} are the minimal, maximal and optimal temperature for chilling
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186 period. R_f is calculated with a similar sigmoid function as used in TTM^* :

$$R_f(D) = \begin{cases} 0 & \text{if } S_c < C^* \\ \frac{a}{1 + e^{-b(T-c)}} & \text{if } S_c \geq C^* \end{cases} \quad (9)$$

188 As above for TTM , to test for the importance of the rate function formulation, a
189 second version of SM (named SM^*) was employed with different equations to
190 calculate R_f and R_c as below:

$$R_f(D) = \begin{cases} 0 & \text{if } T(D) \leq T_b \text{ or } S_c < C^* \\ T - T_b & \text{if } T(D) > T_b \text{ and } S_c \geq C^* \end{cases} \quad (10)$$

$$R_c(D) = \begin{cases} 0 & \text{if } T(D) \leq T_c \\ T - T_c & \text{if } T(D) \geq T_c \end{cases} \quad (11)$$

193 where T_c is critical temperature. We have eight parameters in SM (T_{\min} , T_{\max} , T_{opt} , a , b ,
194 c , C^* and F^*), and four parameters in SM^* (T_b , T_c , C^* and F^*)

195 **2.2.4 Parallel model (PM)** (Landsberg, 1974; Hänninen, 1990; Kramer, 1994).

196 PM assumes that the effect of forcing temperature on budburst can take place even
197 during the chilling. R_c is calculated as in SM (Eq. 8), whereas R_f is calculated with the
198 following equation, a modification of Eq. 9 of SM :

$$R_f(D) = \begin{cases} 0 & \text{if } D < t_0 \\ k \frac{a}{1 + e^{-b(T-c)}} & \text{if } D \geq t_0 \end{cases} \quad \text{and} \quad k = \begin{cases} K_m + \frac{1 - K_m}{C^*} S_c & \text{if } S_c < C^* \\ 1 & \text{if } S_c \geq C^* \end{cases} \quad (12)$$

200 where K_m is a model parameter. PM has one more parameter (K_m) than SM .

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2.2.5 Alternating model (AM) (Murray et al., 1989).

AM has the same rate of forcing as TTM (Eq. 5) but fixed t_0 on the January 1st. The chilling rate equals the number of chilling days (Eq. 13), with start of chilling fixed on November 1st. The start of forcing and chilling did as previous study (Murray et al., 1989)

$$R_c(D) = \begin{cases} 0 & \text{if } T(D) > T_c \\ 1 & \text{if } T(D) \leq T_c \end{cases} \quad (13)$$

The major difference between AM and the other models is the definition of F^* (Eq. 3), which in AM is not a constant parameter but a negatively exponential function of the state of chilling (Eq.14) (Cannell and Smith, 1983; Hänninen, 1990). In this way, flexibility is introduced in modeling the budburst process as the forcing period is controlled by the chilling period.

$$F^*(D) = f_a + f_b \times e^{-f_c \sum_{t_0}^D R_c} \quad (14)$$

Where f_a, f_b, f_c are fitting parameters. AM has five parameters (T_b, T_c, f_a, f_b, f_c).

2.2.6 Unified model (UM). (Chuine, 2000)

UM combines features of the other models and merges the equations for R_c and R_f into one sigmoid equation:

$$\frac{1}{1 + e^{a(T-c)^2 + b(T-c)}} = \begin{cases} R_c(D) & \text{if } a = C_a \text{ and } b = C_b \text{ and } c = C_c \\ R_f(D) & \text{if } a = 0 \text{ and } b = F_b \text{ and } c = F_c \end{cases} \quad (15)$$

where C_a, C_b and C_c are chilling rate parameters, F_b and F_c are forcing rate parameters.

In UM, t_{1c} is assumed on September 1st. The forcing units start to accumulate when a sufficient amount of chilling has occurred (C^*), and F^* is calculated with an

222 exponential function of R_c similarly to Eq. 14 from t_{1c} to t_{2c} ,

$$F^*(D) = \omega \times e^{-k \sum_{t_{1c}}^{t_{2c}} R_c} \quad (16)$$

224 where k , w and t_{2c} are model parameters. The unified model has nine parameters (C_a ,
225 C_b , C_c , F_b , F_c , C^* , k , w , t_{2c}).

226 **2.3 Parameter estimation and Bayesian Model comparison**

227 Parameters were estimated with Bayesian calibration (BC) using the version of
228 Markov Chain Monte Carlo (MCMC) known as the Metropolis-Hastings random
229 walk (Robert and Casella, 2004). Bayes' theorem can be written as a simplified form:

$$p(\theta | BB) \propto p(BB | \theta) p(\theta) \quad (17)$$

231 Where BB is the budburst observation, $p(\theta | BB)$ is the posterior distribution of the
232 parameter value θ , $p(BB | \theta)$ is the likelihood function for θ and the factor $p(\theta)$ is
233 the prior distribution for θ (Sparacino G, 2000; Van Oijen et al, 2005).

234 (i) Prior. The prior parameter information can be obtained directly from
235 measurements or derived from the literature. In our case, the initial values of the
236 parameters were derived from the literature (Kramer, 1994; Chuine et al., 1998;
237 Linkosalo et al., 2008) or set subjectively. The initial uncertainty of each parameter is
238 quantified in terms of a prior probability distribution with lower and upper bounds.
239 We assumed the distribution as uniform and non-correlated.

240 (ii) Data likelihood. The data likelihood (Li) function is determined by the model
241 errors, i.e. the difference between the simulated and observed output variable, in this
242 case the budburst. The likelihood is computed assuming measurement errors are

243 Gaussian and uncorrelated (Van Oijen et al, 2005).

$$L_i = \prod_{i=1,n} \frac{1}{\sigma_i \sqrt{2\pi}} \exp \left[-\frac{1}{2} \left(\frac{M(\theta)_i - BB_i}{\sigma_i} \right)^2 \right] \quad (18)$$

245 Where BB_i is the budburst observed in sampling year i , $M(\theta)_i$ is the simulated
246 budburst value, and σ_i the standard deviation of the model error. The observed
247 budburst dates were obtained from the RMI. For this BC, we only used data from the
248 sites with the most observations (Table 1).

250 (iii) Posterior. The posterior distribution was determined using MCMC as follows:

251 The budburst model was run 10^5 times with different parameter settings. This was
252 done by a walk through the parameter space in such a way that the collection of
253 visited points formed a representative sample from the posterior distribution for the
254 parameters. The first step in this walk of the MCMC was to run an initial simulation
255 with parameter values from a fixed starting point, and to calculate the total data
256 likelihood of that point with Eq. 18. The second step was to generate a proposal for a
257 new candidate parameter vector value θ' by adding a vector of random numbers to
258 the previous parameter vector θ , and then evaluate the data likelihood at that point.

259 The candidate point was accepted as part of the posterior distributions if the
260 Metropolis-ratio (equation 19) of the corresponding data likelihood values and the
261 data likelihood of the previous accepted point was larger than a uniform (0, 1) random
262 variable u .

$$\beta = \frac{p(\theta' | D)}{p(\theta_i | D)} = \frac{p(D | \theta')}{p(D | \theta_i)} \quad (19)$$

264 The simplification shown in Eq. 19, with the Metropolis ratio being equal to the ratio

1 265 of likelihoods, is valid because our prior parameter probabilities are from uniform
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3 266 distributions and thus cancel out. The Bayesian calibration scheme generates two
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6 267 chains, one with parameter vectors (which represent a sample from the posterior
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9 268 distribution) and a chain with the corresponding model outputs. The BC does not only
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11 269 provide the best fit, where the likelihood was highest, but reduced uncertainty about
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14 270 parameter values, as expressed in the posterior joint probability distribution (Van
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17 271 Oijen et al., 2005).

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20 272 After BC, we can use the posterior parameter distribution for model comparison by
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22 273 means of Bayesian model comparison (BMC). In our case, we divided the database of
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25 274 available budburst observations into two sub-datasets. We used one sub-dataset to do
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28 275 BC as described above, and generated the posterior 10^5 parameter vectors.
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31 276 Subsequently, the studied models were run using these posterior parameter values and
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34 277 tested against the second sub-dataset. The first subset is for the most complete and the
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37 278 second is the remaining data. The model output generated in this second step was
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39 279 used to calculate the data likelihood for each run using Eq. 18. The average of the 10^5
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42 280 likelihoods \bar{L} was calculated. After having calculated the average likelihood \bar{L}_j
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45 281 for model M_j , we calculate the posterior probability for each model as:
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$$P(M_i | D) = \bar{L}_i / \sum_{j=1}^n \bar{L}_j \quad (20)$$

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53 284 Where n is the number of models that we compared. Equation 20 presupposes that
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56 285 there was no prior preference for any of the models, i.e. the prior probabilities for the
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59 286 different models were all equal. The different values of $P(M_j|D)$ tell us the relative
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1 287 probability of model M_j being the correct one, compared with the other models. More
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4 288 detail can be found in Kass and Raftery (1995) and a simple tutorial is given by Van
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6 289 Oijen (2008).

9 290 **2.4 Root Mean Square Error**

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12 291 In addition to BMC, the model performance with best-fit parameters (i.e. the
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15 292 parameter vectors from the posterior samples with maximum likelihood) was
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18 293 estimated with the root mean square error (RMSE) between the predicted and the
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21 294 observed budburst values:

$$24 \quad 295 \quad RMSE = \sqrt{\frac{\sum_{i=1}^n (M(\theta)_i - BB_i)^2}{m-1}} \quad (21)$$

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29
30 296 Where $M(\theta)_i$ and BB_i are defined as in Eq. 18, and m is the number of observations.
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33 297 The RMSE of predictions was calculated for (i) the same dataset of budburst
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36 298 observations used for parameter estimation, i.e. for BC (called hereafter internal
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39 299 RMSE, $RMSE_{\text{internal}}$) and (ii) an independent dataset, i.e. the same dataset was used
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41 300 for BMC (external RMSE, $RMSE_{\text{external}}$).

3. Results

3.1 Root Mean Square Error

The RMSE values of predictions are shown for all the models in Table 3. The details of parameter values can be found in Appendix B.

According to the $RMSE_{internal}$, TTM, TPFM, SM and UM are all reliable models for the studied four species, with RMSE values all smaller than for NM (Null model, i.e. using the mean of observations as predictor), except for the TTM for beech and UM for birch. The smallest $RMSE_{internal}$ values were obtained with the TTM for birch and chestnut (3.91 for birch, 5.47 for chestnut), and SM for oak and beech (4.53 for oak, 6.92 for beech). For AM and PM, the performance was poor, with $RMSE_{internal}$ values being even larger than NM. On average, the $RMSE_{internal}$ values of the different models followed the ranking $SM < TPFM = TTM < UM < NM < AM < PM$ across the studied four species.

The $RMSE_{external}$ showed that TTM, TPFM and SM were still the most reliable models as shown by the $RMSE_{internal}$. However, the $RMSE_{external}$ of UM is poor. The best fitting models differed among species. The TTM was still the best model for chestnut, but not for birch for which the best model was SM. TPFM gave the smallest external RMSE for oak and beech. For beech, the external RMSE of all models were greater than the RMSE associated with the Null model, suggesting that none of these models could effectively reproduce the timing of budburst in beech trees. For two-phase models, both internal and external RMSE suggested the model performance did not relate to the model complex, i.e. number of parameters.

1 323 **3.2 Bayesian model comparison**

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3 324 The model probabilities calculated with BMC are shown in Table 4. The model
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6 325 probabilities gave similar results as model comparison using the RMSE. The TTM,
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9 326 TPFM and SM have high probabilities. For the other models, the probabilities were
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12 327 close to zero. For beech and oak, the highest probability was associated to TTM,
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15 328 whereas for birch and chestnut to TPFM. The SM is the third best model for the
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18 329 studied four species. Across species, the average model probabilities show that TPFM
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21 330 is the best model, which has a bit better performance than TTM, and SM is still the
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24 331 best two-phase models. The BMC also suggested model performance did not relate to
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27 332 the model complex, i.e. number of parameters.

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30 333 **3.3 Impact of different rate function on model performance**

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32 334 The analysis with different temperature rate function was limited to only one (well
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35 335 performing) one-phase model and one (well performing) two phases model, i.e. TTM
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38 336 and SM. The TTM*, using a sigmoid function for forcing temperature, had a slightly
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41 337 larger internal and external RMSE than the simple TTM (Table 3), indicating that the
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44 338 complicated sigmoid temperature function did not improve model performance. The
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47 339 SM*, using a linear dependency for both chilling and forcing temperature, exhibited
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50 340 considerably larger internal and external RMSE values, suggesting that the linear
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53 341 temperature function did not capture well the response to temperature during bud
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56 342 dormancy for these species. The BMC model probabilities gave very similar results.
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59 343 Though the probabilities to be correct of the modified models are not zero (0.1-0.25),
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62 344 these probabilities were always lower than the ones associated with the original

1 345 models.

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5 346 **3.4 Parameter estimation**

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7 347 TPFM was supposed to be the best model for birch and chestnut, and second best for
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10 348 oak and beech. Parameter estimations for TPFM showed that the last month prior to
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13 349 budburst had the greatest impact on determining the date of bud opening in the case of
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16 350 birch (23days preceding budburst) and chestnut (29days). This period of most
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19 351 influence extended to the last three months prior to budburst for the later flushing
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22 352 species, i.e. oak (79days) and beech (88days) (Appendix B). In the SM, chilling was
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24 353 allowed to occur within a wide range of temperature. The chilling remained close to
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27 354 unity throughout the entire range of actual winter temperatures.

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29 355 Parameter estimates are shown in Appendix B. Only the parameters of TPFM and SM
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32 356 (the best performing models) were further analyzed: their uncertainty, prior and
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35 357 posterior distributions, best-fit parameters with standard deviation and parameter
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38 358 correlation are reported in Appendix C. A detailed parameter analysis for UM is
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41 359 reported in Fu et al. (2012). The ranges of the posterior parameter coefficients are
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44 360 typically narrower than the prior parameter coefficient ranges, suggesting that the
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47 361 Bayesian calibration reduced the uncertainty of the parameter coefficients. However,
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49 362 not all parameter coefficients exhibited a significant reduction.

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4. Discussion :

4.1 $RMSE_{internal}$ vs $RMSE_{external}$

As expected $RMSE_{external}$ was always larger than $RMSE_{internal}$. The difference of the two RMSEs shows the ability of a given model to adjust to variation in the data. A large difference suggests that even though the model can be fitted to one dataset, the derived parameter values depend on the data used for parameterization (Linkosalo et al., 2008). Trees of the same species but growing at different sites are exposed to many different conditions, which are likely affecting the timing of budburst, such as soil fertility (Wielgolaski, 2001), humidity (Friedel et al., 1993; Kramer et al., 2000; Wielgolaski, 2001), elevation or climate (Kramer, 1995; Spano et al., 1999). Moreover, trees at different sites may also differ genotypically, and thus differ in the phenological response to climate (Kramer, 1995; Myking and Heide, 1995; Leinonen and Hanninen, 2002). These factors make local adaptation possible and therefore local populations may leaf out at different days of the year. Furthermore, in our study, the data of air temperature were unfortunately not available at the sites but were derived from nearby weather stations, through interpolation. This procedure might have introduced some further undesired site variability because of small differences in landscape and topography between the nearest weather stations and the investigated trees. All these factors probably worsened model predictions and contributed to the poor external validation when testing the models with independent data from different sites. Additionally, it is worth to note that the models were not designed for the four species or not all of them (e.g. TTM was originally constructed for *Picea sitchensis* r

1 387 (Cannell and Smith, 1983)). Even small species-specific differences in the budburst
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3 388 process might result in large simulation biases in these rather empirical modeling
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6 389 approaches.

9 390 **4.2 The advantage of Bayesian procedure**

11 391 *Bayesian calibration.* Bayesian calibration estimates the most likely probability
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13 392 distributions of the model parameters with regard to the likelihood of the model
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16 393 output being equal to the observations. Therefore, Bayesian calibration can deal with
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19 394 a large number of parameters simultaneously, associates prior knowledge on
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22 395 parameters with measurements of output variables, and can markedly reduce
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25 396 parameter uncertainty especially when there is insufficient knowledge on the prior
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28 397 parameter distribution (Fu et al., 2012; Van Oijen et al 2006; 2012). However, the
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31 398 uncertainty associated to parameters obtained by fitting procedures is generally high
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34 399 for budburst models because many factors affecting budburst remain unknown or not
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36 400 fully explained (e.g. the role of the non-structural carbohydrate of reserve (Morin et
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38
39 401 al., 2007) and of photoperiod, see below) and direct parameter measurements lack. In
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42 402 our study, the low number of parameters of the budburst models calibrated (maximum
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44 403 9 parameters) contributed to obtain a significant reduction in parameter uncertainty
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47 404 (as shown in Appendix C). The posterior distributions of some parameters did not
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50 405 follow a normal distribution, introducing difficulties to identify the optimal values.
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53 406 Hence, we selected as the optimal value the parameter values for which likelihood
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55 407 was maximum.

58 408 *Bayesian model comparison.* RMSE and BMC give a quantitative assessment of

1 409 model performance, and are a good criterion for comparison of different models. The
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3 410 traditional Root Mean Square Error method considers only the best fit model
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5 411 parameter vector. However, BMC does evaluate parameter uncertainty and their
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7 412 influence on prediction uncertainty. We clarify this with an example. For oak, the
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9 413 $RMSE_{\text{internal}}$ obtained with SM is smaller than that obtained with TPFM (Table 3).
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11 414 Thus, intuitively, one would prefer SM over TPFM. However, BMC model
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13 415 probabilities show that TPFM has a higher probability of being correct than SM. This
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15 416 is because uncertainty associated to SM is higher than the uncertainty associated to
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17 417 TPFM. One should therefore prefer the TPFM over the SM.
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28 419 **4.3 Model comparison**

29 420 In our study, we found the simple one-phase models (i.e. models without chilling
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31 421 requirement but only forcing temperature), such as TTM and TPFM, to be the best
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33 422 models to reproduce the timing of budburst. These results are consistent with other
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35 423 studies (Hunter and Lechowicz 1992; Linkosalo et al, 2008; Leinonen and Hanninen,
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37 424 2002). In particular, Leinonen and Kramer (2002) also found that chilling is not so
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39 425 important for good performance of models. The good predictive capacity of the
40
41 426 Thermal Time model or Thermal period fixed model implies that the buds may be
42
43 427 already sufficiently chilled when the process leading to bud opening is modeled to
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45 428 start. Among the two-phase models, the sequential model performed better than the
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47 429 others. This is also consistent with previous studies (e.g. see Kramer 1994 for beech)
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49 430 and suggests that modeling of chilling and forcing processes in an orchestrated,
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1 431 sequential way is closer to reality than parallel, alternating or unified modeling
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3 432 approaches. However, the two-phase models showed overall a poorer performance
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6 433 than the one-phase. This is likely to be partially caused by over-parameterization
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9 434 (Linkosalo et al., 2008).

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11 435 Previous comparisons of the different models suggested that no model is superior for
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14 436 all species and should be put forward as consensus model (Hunter and Lechowicz,
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17 437 1992; Chuine et al., 1998; Fu et al., 2012). However, we observed common pattern
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20 438 between the two late flushing, late-successional species and the two early flushing,
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23 439 earlier successional species. In fact, budburst of beech and oak was best simulated by
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25 440 TTM, whereas budburst of birch and chestnut was best simulated by TPFM.
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28 441 Furthermore, the parameter analysis suggested that spring temperature correlated with
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31 442 budburst in a different way for earlier and late flushing / successional species, with
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34 443 large forcing accumulated for oak and beech than for birch and chestnut. Though the
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36 444 one-phase model can satisfactory predict the budburst date (see above), the difference
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39 445 between earlier and late successional species may require different modelling
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42 446 approaches to improve the model performance. Late successional species are expected
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45 447 to have a more complex approach to budburst than early successional species (Körner
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48 448 and Basler, 2010). For instance, good performances of two-phase thermal models
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51 449 were recently reported for late successional species (Thompson and Clark, 2008;
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53 450 Morin et al., 2009; Vitasse et al., 2011). Furthermore, the budburst of late successional
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56 451 species might be more sensitive to environmental cues other than temperature, as
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58
59 452 photoperiod. This is described in detail below.

1 453 **4.4. Other environmental factors influencing budburst**

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3 454 The fact that the performance of the models was overall not outstanding indicates that
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6 455 environmental factors other than temperature might play an important role in the
7
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9 456 budburst process of the investigated species. Although many factors remain unknown
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12 457 in our understating of tree phenology, experimental evidences and modeling exercises
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15 458 have indicated that photoperiod might be an important regulator of budburst in certain
16
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18 459 tree species (Linkosalo et al., 2006; Chuine et al., 2010; Körner and Basler, 2010). In
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20
21 460 general, a ‘short photoperiod’ threshold may inhibit budburst in extreme warm spring
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24 461 conditions (to avoid trees to have budburst too early), whereas a ‘long photoperiod’
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27 462 threshold may stimulate budburst in extreme cold spring conditions (to avoid trees to
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30 463 have budburst too late). This photoperiod sensitivity might be species-specific, with
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33 464 again similarities between late flushing late successional species and earlier flushing
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36 465 earlier successional species. For instance, Fu et al. (unpublished) found that budburst
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39 466 progressively advances with spring warming intensity in early successional species as
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42 467 birch, whereas it does not for late successional species as beech and oak, which seem
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45 468 to have a ‘short photoperiod’ threshold’. Nevertheless, as photoperiod-driven budburst
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48 469 models do not always improve the model performance of temperature-driven models
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51 470 (e.g. see for beech Kramer 1994) and more experimental studies are needed to provide
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53
54 471 sound modeling ground for this matter, the lack of photoperiod control in the models
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56
57 472 used for this methodological comparison does not represent a major drawback.

58 474 **4.5 Budburst shift under climate warming**

1 475 A future increase in temperatures is more than likely (IPCC, 2007) and earlier dates of
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3 476 budburst are already commonly observed in many plant species (Menzel et al., 2006;
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6 477 Linkosalo et al., 2008). However, this shift might not occur in all species, because of
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8
9 478 the different requirements for chilling and forcing temperature to release winter
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11 479 dormancy (Cannell and Smith, 1986). If climatic warming implies insufficient chilling,
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14 480 then the buds will remain partially dormant in spring and will require a larger thermal
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17 481 time to initiate budburst (Murray et al., 1989; Linkosalo et al., 2008; Harrington et al.,
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19
20 482 2010). The date of budburst in a warmer climate could thus remain unchanged or even
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23 483 be postponed. On the other hand, if the chilling requirement of a species is currently
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26 484 far exceeded, then the required chilling will likely also be easily reached under
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29 485 conditions of climatic warming, and budburst will occur much earlier than at present
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32 486 because of the enhanced temperature during forcing. In our study, we found that the
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35 487 timing of budburst for the studied four species can be successfully reproduced using
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38 488 the one-phase models in which only forcing temperature was involved. This suggested
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41 489 that the chilling may be sufficient in the present climate for each species. However,
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44 490 further research on chilling requirement is needed to evaluate whether climate
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47 491 warming will induce an advancement of budburst (chilling requirements low and met
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50 492 even in warmer climate) or not (chilling requirements high and not met in a warmer
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53 493 climate).

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5. Conclusion

(1) Our results suggest that the one-phase models (only considering forcing) have higher probabilities of being correct than the two-phase models (accounting for both forcing and chilling) for all the four studied species. Furthermore, these results suggest that the chilling requirement is easily met in Belgium, and therefore predicting budburst may rely only on the forcing temperature. However, this might change with global warming.

(2) The probability of TTM is the highest for the late flushing and late successional beech and oak, whereas TPFM is the most plausible model for the earlier flushing and earlier successional birch and chestnut. The SM is the third best model for the studied four species. For the other models, the probabilities were close to zero. As expected more complex (two-phase) models performed better for late flushing / late successional species but this effect was minor. Addition of photoperiod might further improve budburst simulation for late flushing / late successional species.

(3) Model performance varies when evaluated with BMC or RMSE. Bayesian model probability is however the best criterion for model comparison since both accuracy and uncertainty are evaluated, in contrast to the Root Mean Square Error which only compares observations with model results achieved with the best-fitting parameter vector.

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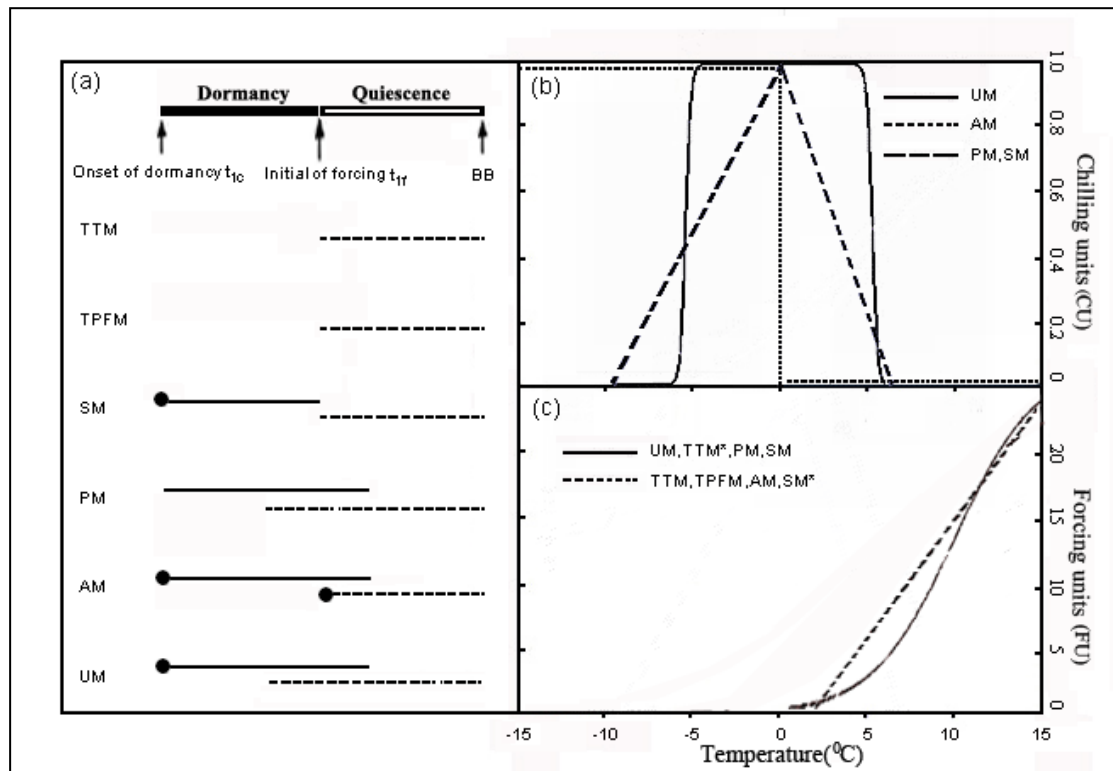
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Figure 1. A schematic representation of (a) the basic different modelling approaches concerning the periods when buds are affected by forcing temperature (dashed line) and chilling temperature (continuous line), (b) the chilling rate function and (c) the forcing rate function (figure modified from Chuine 2000). BB is budburst. A dot means the day is fixed. TTM is Thermal Time model, TPFM is Thermal Period Fixed model, SM is Sequential model, PM is Parallel model, AM is Alternating model and UM is Unified model.



1 **Table 1.** Characteristics of the studied species. The numbers in parentheses following
2 the observation site names are the number of observational years in the study sites
3 (not all species-site combinations have data for the entire period considered). Period
4 considered was from 1958 to 1998.

5

6 **Table 2.** Characteristics of the studied sites. Annual temp is the mean annual
7 temperature, calculated at each site from 1958 to 2002.

8

9 **Table 3.** Root mean square error for the validation using the same dataset used for
10 calibration ($RMSE_{\text{internal}}$) and using an independent dataset ($RMSE_{\text{external}}$) of 8
11 budburst models and a null model (NM) which assumes that budburst occurs on the
12 average DOY of observed budburst in the fitting dataset. The symbol n indicates the
13 number of observations used to fit and validate the models. The best model
14 performance per species is shown in bold. Average is the numerical mean of RMSE
15 across species. TTM is Thermal Time model, TTM* is Thermal Time model using
16 sigmoid forcing rate function, TPFM is Thermal Period Fixed model, SM is
17 Sequential model, SM* is Sequential model using linear chilling and forcing rate
18 function, PM is Parallel model, AM is Alternating model and UM is Unified model.

19

20 **Table 4** Conditional probabilities (ranging between 0 and 1) of different models
21 calculated using Bayesian model comparison. Details on the studied models can be
22 found in the text. Average is the numerical mean of conditional probabilities across
23 species. TTM is Thermal Time model, TTM* is Thermal Time model using sigmoid
24 forcing rate function, TPFM is Thermal Period Fixed model, SM is Sequential model,
25 SM* is Sequential model using linear chilling and forcing rate function, PM is
26 Parallel model, AM is Alternating model and UM is Unified model.

1 **Table 1.** Characteristics of the studied species. The numbers in parentheses following
 2 the observation site names are the number of observational years in the study sites
 3 (not all species-site combinations have data for the entire period considered). Period
 4 considered was from 1958 to 1998.

Species	Latin name	Budburst period	Fitting dataset	Validation dataset
			Site	Site
Birch	<i>Betula verrucosa</i> <i>Ehrn.</i>	18Apr. ±10	Blanmont (31)	Bastogne (10)
				Dinant(13)
				Leopoldsburg (3)
				Xhendremael (10)
Chestnut	<i>Aesculus</i> <i>hippocastanum</i> L.	17Apr. ±12	Blanmont (36)	Bastogne (17)
				Leopoldsburg (9)
				Xhendremael (2)
Oak	<i>Quercus robur</i> L.	5May.±8	Blanmont (22)	Bastogne (9)
				Leopoldsburg (5)
				Xhendremael (9)
Beech	<i>Fagus sylvatica</i> L.	1May. ±9	Bastogne (19)	Dinant (11)
				Leopoldsburg (5)
				Xhendremael (12)

5

6

1 **Table 2.** Characteristics of the studied sites. Annual temp is the mean annual
2 temperature, calculated at each site from 1958 to 2002.

site	coordinates	Elevation (m)	Annual temp.(°C)
Bastogne	50°00'22"N, 5°43'14"E	476	8.42
Blanmont	50°37'21"N, 4°38'20"E	125	12.19
Dinant	51°15'42"N, 4°54'35"E	163	9.60
Leopoldsburg	51°07'03"N, 5°15'42"E	31	10.41
Xhendremael	50°42'16"N, 5°28'43"E	120	12.71

3

4

1 **Table 3.** Root mean square error for the validation using the same dataset used for
2 calibration ($RMSE_{\text{internal}}$) and using an independent dataset ($RMSE_{\text{external}}$) of 8
3 budburst models and a null model (NM) which assumes that budburst occurs on the
4 average DOY of observed budburst in the fitting dataset. The symbol n indicates the
5 number of observations used to fit and validate the models. The best model
6 performance per species is shown in bold. Average is the numerical mean of RMSE
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8 sigmoid forcing rate function, TPFM is Thermal Period Fixed model, SM is
9 Sequential model, SM* is Sequential model using linear chilling and forcing rate
10 function, PM is Parallel model, AM is Alternating model and UM is Unified model.

Species	RMSE	n	TTM	TTM*	TPFM	SM	SM*	PM	AM	UM	NM
Birch	$RMSE_{\text{internal}}$	31	3.9	5.7	4.6	5.6	6.5	12.1	7.6	8.9	5.7
	$RMSE_{\text{external}}$	23	10.7	11.8	12.0	9.7	11.6	12.3	10.7	15.9	12.0
Chestnut	$RMSE_{\text{internal}}$	36	5.5	6.3	6.3	6.8	7.7	10.3	7.0	5.6	8.8
	$RMSE_{\text{external}}$	19	10.6	10.7	11.9	12.5	10.9	13.9	11.2	12.6	15.7
Oak	$RMSE_{\text{internal}}$	21	4.8	5.9	5.6	4.5	7.1	7.1	8.4	4.8	5.8
	$RMSE_{\text{external}}$	23	8.7	8.6	8.1	9.6	10.8	25.9	9.3	10.3	10.0
Beech	$RMSE_{\text{internal}}$	19	9.9	10.7	8.7	6.9	8.5	8.6	11.2	7.9	9.8
	$RMSE_{\text{external}}$	28	8.9	11.2	8.5	11.0	11.4	24.4	15.4	12.9	7.3
average	$RMSE_{\text{internal}}$		6.4	7.2	6.3	6.0	7.4	9.5	8.5	6.8	7.5
	$RMSE_{\text{external}}$		9.7	10.6	10.1	10.7	11.2	19.1	11.6	12.9	11.2

11

12

1 **Table 4** Conditional probabilities (ranging between 0 and 1) of different models
2 calculated using Bayesian model comparison. Details on the studied models can be
3 found in the text. Average is the numerical mean of conditional probabilities across
4 species. TTM is Thermal Time model, TTM* is Thermal Time model using sigmoid
5 forcing rate function, TPFM is Thermal Period Fixed model, SM is Sequential model,
6 SM* is Sequential model using linear chilling and forcing rate function, PM is
7 Parallel model, AM is Alternating model and UM is Unified model. The best model
8 performance per species is shown in bold.

Models	Beech	Oak	Birch	Chestnut	average
TPFM	0.18	0.20	0.35	0.41	0.29
TTM	0.28	0.25	0.23	0.23	0.25
TTM*	0.26	0.22	0.18	0.13	0.20
SM	0.13	0.16	0.14	0.10	0.13
SM*	0.11	0.10	0.06	0.08	0.09
PM	0.01	0.01	0.00	0.00	0.01
AM	0.04	0.05	0.03	0.05	0.04
UM	0.01	0.01	0.01	0.00	0.01

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