

ORIGINAL ARTICLE

Effects of climatic warming on spring phenology in subtropical trees: process-based modelling with experiments designed for model development

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33 **Abstract**

35 We developed process-based tree phenology models for four subtropical tree species, and for the
 36 first time for these trees, we based the model development on explicit experimental work
 37 particularly designed to address the processes being modelled. For all the four species, a model of
 38 seedling leafout was developed, and for *Torreya grandis*, a model for female flowering in adult
 39 trees was additionally developed. The models generally showed reasonable accuracy when tested
 40 against two sources of independent data. In scenario simulations, the models projected an advanced
 41 spring phenology under climatic warming for 2020 – 2100. For the leafout of seedlings, the
 42 advancing rates varied between 4.7 and 5.9 days per one °C warming, with no major differences
 43 found between the climatic scenarios RCP4.5 and RCP8.5. For *Torreya* flowering, less advancing
 44 was projected, and the projected advancing per one °C warming was less for RCP8.5 (0.9 days / °C)
 45 than for RCP4.5 (2.3 days / °C). The low advancing rates of *Torreya* flowering were caused by
 46 reduced chilling under the warming climate and by the particular temperature responses found for
 47 *Torreya* flowering. These findings highlight the need to base the model development on explicit
 48 experiments particularly designed to address the process modelled.

50

51 **KEYWORDS**

52 bud burst, chilling requirement, climatic warming, flowering, leafout, ontogenetic development,
53 phenology, process-based modelling, rest break, subtropical trees

54

55 1 | INTRODUCTION

56 In the terrestrial biomes of the world, shifts in the spring phenology of plants are among the most
 57 important effects of the ongoing climate change (Polgar & Primack, 2011). These changes affect
 58 essential ecosystem processes, such as the cycling of water, carbon and nutrients (Kramer &
 59 Hänninen, 2009; Richardson et al., 2009), ecosystem productivity (Keenan et al., 2014), plant-
 60 animal relationships (Senior, Evans, Leather, Oliver, & Evans, 2020), population dynamics and
 61 competition of plant and animal species (Delpierre, Guillemot, Dufrêne, Cecchini, & Nicolas, 2017;
 62 Zettlemoyer, Schultheis, & Lau, 2019), and ultimately, shifts in the geographical ranges of species
 63 (Chuine & Beaubien, 2001; Chuine, 2010). Analyses of long-term phenological records have
 64 generally shown that warming has caused advanced phenological development in spring over the
 65 past few decades (Menzel et al., 2006; Zheng et al., 2016). However, the sensitivity of the
 66 phenological development to rising temperatures has been found to decrease at the same time, so
 67 that the advancing trends of spring phenology have been levelling off in several cases (Fu et al.,
 68 2015a). This has been attributed to the effects of reduced chilling, also caused by climatic warming
 69 (Murray, Cannell, & Smith, 1989; Fu et al., 2015b; Ford, Harrington, Bansal, Gould, & St Clair,
 70 2016; Luedeling, 2012; Martínez-Lüscher, Hadley, Ordidge, Xu, & Luedeling, 2017, Wang et al.,
 71 2020;), or to the restricting effect of photoperiod, which is not changed by climatic warming
 72 (Vitasse & Basler, 2013; Fu et al., 2015a, 2019a,b).

73

74 After growth cessation in autumn, the buds of boreal and temperate trees attain the state of rest
 75 (endodormancy; Lang, Early, Martin, & Darnell, 1987), where bud burst and growth onset are
 76 prevented by physiological factors inside the buds (Perry, 1971; Fuchigami, Weiser, Kobayashi,
 77 Timmis, & Gusta, 1982; Hänninen & Tanino, 2011). The growth-arresting conditions are removed
 78 by prolonged (days to months) exposure to low chilling temperatures (Rohde & Bhalerao, 2007;
 79 Cooke, Eriksson, & Junttila, 2012; Tylewicz et al., 2018), traditionally, temperatures near +5 °C

80 have been regarded as necessary for chilling (Sarvas, 1974). This is the chilling requirement of rest
 81 completion (Hänninen, 1995, 2016), which prevents a premature growth onset during mild periods
 82 in autumn and winter, which would lead to frost damage during subsequent periods of frost
 83 (Cannell, 1985; Hänninen, 1991; Zohner, Mo, Sebald, & Renner, 2020), a phenomenon more
 84 recently called ‘false springs’ (Marino, Kaiser, Gu, & Ricciuto, 2011; Chamberlain, Cook, de
 85 Cortázar-Atauri, & Wolkovich, 2019). After the chilling requirement is met, the phase of quiescence
 86 (ecodormancy, Lang et al, 1987) is attained (Perry, 1971; Fuchigami et al., 1982; Hänninen &
 87 Tanino, 2011). During quiescence, bud burst and growth onset are prevented by low air
 88 temperatures only, so that ontogenetic development, i.e., microscopic anatomic changes within the
 89 buds towards bud burst, occurs in relatively high growth-promoting forcing temperatures (Sarvas
 90 1972, 1974). Visible bud burst occurs as a result of prolonged (days to months) exposure to forcing
 91 temperatures (the high-temperature requirement of growth onset, Hänninen, 1995, 2016).

92

93 The effects of high temperatures on the spring phenology of plants have been addressed in
 94 quantitative terms with various temperature sum calculations since the days of Réaumur (1735), (for
 95 reviews, see Arnold, 1959; Wang, 1960; Chuine, de Cortázar-Atauri, Kramer, & Hänninen, 2013).
 96 Similar chilling-unit calculations for rest break are of more recent origin, but they, too, have a long
 97 history by now (Weinberger, 1950). Since the early 1970s, holistic models addressing both
 98 phenomena simultaneously have been developed for boreal and temperate trees (Sarvas, 1972,
 99 1974; Richardson et al., 1974; Landsberg, 1974; Cannell & Smith, 1983; Chuine, 2000; Harrington,
 100 Gould, & St.Clair, 2010; Chuine et al., 2016). These models, currently known as process-based tree
 101 phenology models, predict the timing of spring phenological events, such as vegetative bud burst or
 102 flowering, on the basis of air temperature data (Hänninen & Kramer, 2007; Chuine et al., 2013).
 103 Sometimes these models also address the effects of photoperiod (Nizinski & Saugier, 1988;
 104 Hänninen, 1995). Since the mid-1980s, process-based tree phenology models have been

105 increasingly used for assessing the effects of the projected climate change (Cannell, 1985;
 106 Hänninen, 1991; Kramer, 1994; Chuine et al., 2016).

107

108 In boreal and temperate trees, the chilling requirement of rest break has been studied for a hundred
 109 years: the phenomenon was first reported by Coville (1920). Given this background, it is surprising
 110 that the rest period and the chilling requirement in subtropical trees have not been experimentally
 111 examined until recently, when Du, Pan, & Ma (2019), Song et al. (2020), and Zhang et al. (2021a)
 112 showed that subtropical trees also exhibit the rest period and the chilling requirement of rest
 113 completion. Further, Zhang et al. (2021a) have recently shown that the air temperature responses of
 114 the dormancy processes in subtropical trees are different from those in the more northern ones. This
 115 points to the importance of developing specific process-based tree phenology models for subtropical
 116 trees. To our knowledge, no process-based model has been developed for any subtropical tree
 117 species by using data from experiments explicitly designed for developing and parameterising the
 118 model. Here, using the experimental results of Zhang et al. (2021a) and some additional
 119 experimental data gathered for the present study, we developed process-based spring phenology
 120 models for four subtropical tree species. The models were tested with three sources of independent
 121 data and then used in scenario simulations to assess the effects of climatic warming on spring
 122 phenology in the four sub-tropical tree species over the years 2020 – 2100. We hypothesised that
 123 due to differences in the dormancy processes addressed by the models, the different species (Zhang
 124 et al., 2021a), different life stages (Vitasse, 2013), and different bud types of a given species (Ma,
 125 Huang, Hänninen, Li, & Berninger, 2020) would respond to the warming differentially. The models
 126 we develop here will facilitate the assessing of the effects of climatic change in subtropical
 127 conditions.

128

129 **2 | MATERIALS AND METHODS**130 **2.1 | Model structure**

131 The process-based tree phenology models developed in the present study simulate the effects of air
 132 temperature on the processes of rest break and microscopic ontogenetic development in the buds
 133 towards bud burst (Figure 1). Each model developed was constructed as a combination of three sub-
 134 models: one for rest break, one for ontogenetic development, and one for mediating the effects of
 135 rest break on the ontogenetic development. This modular model structure facilitates the use of
 136 experimental designs that explicitly address each of the three modelled physiological phenomena at
 137 the whole-tree level (Hänninen et al., 2019).

138

139 Sub-model I addresses the effects of low chilling temperatures on the process of rest break (Figure
 140 1). The momentary rate of rest break, $R_r(t)$, is first calculated as a function of air temperature, $T(t)$:

141

$$R_r(T(t)) = f_1(T(t)) \quad (1)$$

144 where f_1 = the function to be determined on the basis of experimental data (see Section 2.3.2). By
 145 definition, the state of rest break at time instant t , $S_r(t)$, is obtained by integrating the momentary
 146 values of the rate of rest break, $R_r(T(t))$, with respect to time:

147

$$S_r(t) = \int_{t_0}^t R_r(T(t)) dt \quad (2)$$

149

150 where t_0 = the starting moment of the rest period. In practice the integration is carried out by
 151 summing the hourly values of $R_r(T(i))$ calculated on the basis of hourly temperatures, $T(i)$. Rest
 152 completion is predicted to occur when the value of $S_r(t)$ attains 100 %:

153

$$154 \quad S_r(t) = 100 \%$$

155

(3)

156 After rest completion, the value of $S_r(t)$ is set at 100 % for the remaining simulation period, which
 157 ends at the predicted time of bud burst.

158 Sub-model II addresses the effects of high forcing temperatures on the rate of ontogenetic
 159 development after rest completion. That particular rate is called the potential rate of ontogenetic
 160 development, $R_{o,pot}$, because after rest completion the rate of ontogenetic development is no longer
 161 restricted by the rest condition. The momentary $R_{o,pot}$ is calculated as a function of air temperature,
 162 $T(t)$:

$$163 \quad R_{o,pot}(T(t)) = f_2(T(t))$$

164

(4)

165 where f_2 = the function to be determined on the basis of experimental data (see Section 2.3.3).

166

167 Sub-model III addresses the restricting effects of the bud rest status on the rate of ontogenetic
 168 development. These effects are modelled with the aid of the model variable ontogenetic
 169 competence, C_o , which is a multiplier with values ranging from 0 to 1. With $C_o = 0$, there is no
 170 ontogenetic development regardless of the prevailing temperature. At the time of rest completion,
 171 the value of $C_o = 1$ is attained, and the rate of ontogenetic development is then equal to the potential

rate. With values between 0 and 1, ontogenetic development takes place at a reduced rate, as indicated by the decimal of C_o . Ontogenetic competence, C_o , mediates the effects of the rest status onto the ontogenetic development, so that its momentary value is calculated as a function of the state of rest break, S_r :

$$C_o(t) = f_3(S_r(t)) \quad (5)$$

where f_3 = the function to be determined on the basis of experimental data (see Section 2.3.4). Following the definition of the variable ontogenetic competence, C_o , the momentary rate of ontogenetic development, $R_o(t)$ is calculated as

$$R_o(t) = C_o(t) R_{o,pot}(t) \quad (6)$$

By definition, the state of ontogenetic development at time instant t , $S_o(t)$, is obtained by integrating the momentary value of the rate of ontogenetic development, $R_o(T(t))$, with respect to time:

$$S_o(t) = \int_{t_0}^t R_o(T(t), C_o(t)) dt \quad (7)$$

where t_0 = the starting moment of the rest period. In practice the integration is carried out by summing the hourly values of $R_o(T(i))$ calculated on the basis of the hourly temperature, $T(i)$. Bud burst is predicted to occur, and the simulation ends, when the value of $S_r(t)$ attains 100 %:

$$S_o(t) = 100\% \quad (8)$$

193 2.2 | Tree species and experimental data

194 2.2.1 | Material categories

195 Process-based tree phenology models were constructed for four sub-tropical tree species:
 196 *Castanopsis sclerophylla*, *Phoebe chekiangensis*, *Pseudolarix amabilis*, and *Torreya grandis*. For
 197 all species, first-year container seedlings were used in the experiments. With *Torreya*, experiments
 198 were also carried out with twigs detached from adult trees. Accordingly, a total of five process-
 199 based models, each representing the corresponding material category (species, seedling / adult tree),
 200 were constructed. To develop the models, both previously published (Autumn experiments, Zhang
 201 et al., 2021a) and original (Spring experiments) data were used.

202

203 2.2.2 | Autumn experiments for Sub-models I and III

204 In the autumn experiments carried out in 2017 – 2019, the experimental seedlings and twigs were
 205 first subjected to chilling for periods of varying duration, then transferred to growth-promoting
 206 forcing conditions with a constant air temperature of +20 °C (Zhang et al., 2021a). The chilling
 207 treatments were carried out in growth chambers at three constant temperatures: +5 °C, +10 °C, and
 208 +15 °C. In the forcing conditions, a regrowth test was carried out by observing the occurrence and
 209 timing of bud burst (leafout, flowering; see Section 2.2.3). For each observed seedling or twig
 210 showing bud burst, the days to bud burst in the forcing conditions, DBB, was calculated. For each
 211 treatment representing a given duration of chilling at a given chilling temperature, the value of bud
 212 burst percentage, BB%, was calculated.

213

214 2.2.3 | Spring experiments for Sub-model II

215 The effects of the air temperature on the potential rate of ontogenetic development were addressed
 216 in the three spring experiments, carried out in the years 2018 – 2020. Until the start of the
 217 experiment, the experimental seedlings and trees overwintered in natural conditions on the Zhejiang
 218 A&F University campus (30°14'N, 119°42'E) in Hangzhou, southeastern China. In order to make
 219 sure that the actual rate of ontogenetic development observed in the experiment represented the
 220 potential rate, the spring experiments of all the three years 2018 – 2020 were started on 13
 221 February, after all the material categories had met the chilling requirement in natural conditions
 222 (Zhang et al., 2021a). In each year, we transferred ten replicated seedlings of each species from
 223 natural outdoor conditions to forcing growth chambers (E-Lotus Technology Co., Beijing, China)
 224 with several constant air temperatures ranging from 10 to 28 °C (Table 1). At the same time, twigs
 225 of adult *Torreya* trees were sampled on the campus and transferred to the forcing chambers. The
 226 twigs and seedlings were prepared for the experiments in the same way as in the autumn
 227 experiments (Zhang et al., 2021a). In all the forcing chambers, day length was 12 h, PPFD 400
 228 $\mu\text{mol m}^{-2} \text{s}^{-1}$, relative humidity 70-80 %, and concentration of CO₂ 300-400 ppm. Temperature of the
 229 chambers was monitored with iButton (Model DS1912L, Embedded Data Systems Co., Ltd, KY,
 230 USA). Bud burst was observed visually, as had been done in the autumn experiments (Zhang et al.,
 231 2021a). In the seedlings of all four species, the determination of bud burst was based on the stage of
 232 leafout, and in the *Torreya* twigs representing adult trees, on female flowering. Despite these
 233 differences, the term 'bud burst' is used in this report as a generic one in connection with the
 234 standard variables BB% and DBB (Zhang et al., 2021a). For each experimental seedling and twig,
 235 the days to bud burst in the forcing conditions, DBB, was calculated.

236

237 **2.3 | Formulating the models on the basis of experimental data**

238 **2.3.1 | Outline**

The experimental information was introduced to Sub-models I, II, and III via the functions f_1 (Eqn. 1), f_2 (Eqn. 4), and f_3 (Eqn. 5), respectively. Once these functions had been defined and parameterized on the basis of the experimental data, the overall model defined by Eqns. (1) – (8) was operationalized to be used in computer simulations.

2.3.2 | Sub-model I

The rate of rest break at any constant temperature T' , $R_r(T')$ was determined experimentally as follows (Sarvas, 1974):

$$R_r(T') = 100 \frac{1}{\Delta t(T')} \quad (9)$$

where $\Delta t(T')$ = the duration of chilling required for rest completion (meeting the chilling requirement) at the constant temperature T' . Because of the multiplier 100, the unit of R is % h^{-1} , so that the value of $R_r(T')$ indicates how many per cent of the cumulative physiological processes required for rest completion take place within one hour. The value of Δt was determined on the basis of the results of the autumn experiments. First, the values of bud burst percentage, BB%, and days to bud burst, DBB, were plotted against the duration of chilling. By means of the scatter plots thus obtained, the value of Δt needed in Equation (9) was determined by two rules: First, it was required that $BB\% \geq 80\%$ for the chilling duration corresponding to Δt . Second, it was required that the value of DBB decreased to a threshold value, DBB_{RC} , determined by the levelling off of the DBB curve in the +5 °C chilling experiment. To that end, an exponential function f_4 was first fitted to the scatter plot of the +5 °C chilling experiment, representing the DBB value of each seedling/twig as a function of the duration of chilling (Figure S1a):

$$DBB(x) = f_4(x) = y_0 + a_1 e^{-b_1 x}$$

(10)

where DBB is the modelled DBB, x = the duration of chilling (days); and y_0 , a_1 , and b_1 are parameters to be estimated. Next, the first derivative with respect to the duration of chilling of the fitted function was calculated as follows:

$$\frac{dDBB}{dx} = -a_1 b_1 e^{-b_1 x}$$

(11)

In the next step, Δt was determined for the +5 °C chilling treatment as equal to the duration of chilling x where the value of the first derivative is equal to -0.3 (Figure S1a):

$$\frac{dDBB}{dx} = -a_1 b_1 e^{-b_1 x} = -0.3$$

(12)

implying

$$\Delta t = x = \frac{-1}{b_1} \ln \frac{0.3}{a_1 b_1}$$

(13)

Next, the exponential function (Eqn. 10) was fitted to the scatter plots of both +10 °C (Figure S1b) and +15 °C chilling treatments. For them, the value of Δt was determined as the duration of chilling

implying the same value of $DBB = DBB_{RF}$ as was obtained with the +5 °C chilling treatment (Figure S1):

$$\Delta t = x = \frac{-1}{b_1} \ln \frac{DBB_{RF} - y_0}{a_1} \quad (14)$$

The Δt values obtained (Table 2; Figure S2) were plugged into Eqn. (9), thus getting three (for *Castanopsis*, *Phoebe*, and *Pseudolarix* seedlings) or four (for *Torreya* seedlings and twigs) data points for R_r in the temperature range of +5 to +15 °C (see Figure 2 in the Results Section). In that temperature range, the function f_1 in Eqn. (1) was determined by fitting a direct line to the scatter plot representing the observed R_r as a function of temperature. It was assumed that at temperatures below +5 °C, R_r would drop from its maximum value (obtained at +5 °C) to zero at -3.4 °C (Sarvas, 1974). If extrapolation was also needed at the high temperature end, it was similarly assumed that R_r would drop from its value at +15 °C to zero at +20 °C. In a sensitivity analysis addressing the uncertainty caused by the lack of data for temperatures under +5 °C, a modified model was used. In that model it is assumed that at any temperature below +5 °C, R_r has a constant value, identical to the maximal value of R_r at +5 °C (see Figure 2 in the Results Section).

2.3.3 | Sub-model II

For Sub-model II, the potential rate of ontogenetic development at any constant temperature T' , $R_{o,pot}(T')$, was determined experimentally as follows (Sarvas, 1972; Campbell, 1978):

$$R_{o,pot}(T') = 100 \frac{1}{DBB(T')}$$

(15)

where $DBB(T') =$ days to bud burst measured at the constant temperature T' after rest completion.

Because of the multiplier 100, the unit of $R_{o,pot}$ is $\% h^{-1}$, so that the value of $R_i(T')$ indicates how many per cent of the ontogenetic changes required for bud burst take place within one hour.

The values of $R_{o,pot}(T')$ were plotted against the experimental temperature T' . The air temperature response of $R_{o,pot}$ (function f_2 in Eqn. 4) was formulated by fitting a sigmoidal function to the scatter plot (see Figure 3 in the Results Section):

$$R_{o,pot}(T) = \frac{a_2}{1 + e^{\frac{1}{b_2}(T - c_2)}}$$

(16)

where T is air temperature and a_2 , and b_2 , and c_2 are parameters to be estimated.

2.3.4 | Sub-model III

By the definition of ontogenetic competence, C_o , (Section 2.1, Eqn. 6), the empirical value of C_o for a given seedling/twig is zero if it shows no bud burst during prolonged forcing, and by the same token, it is unity if its DBB is equal to the DBB representing twigs and seedlings which have just attained rest completion, i.e., equal to $DBB(\Delta t) = DBB_{RC}$ (Figure S1). Between these two extremes, the value of C_o increases proportionally to the ratio of $DBB(\Delta t) / DBB$ of the seedling/twig. In the calculation of the empirical values of C_o , two averaging methods were applied. First, the original DBB observations of the individual twigs/seedlings were replaced by the fitted exponential functions, f_4 (Eqn. 10; Figure S2). Accordingly, the value of C_o for any duration of chilling x at a

given constant chilling temperature was calculated as the ratio $f_4(\Delta t) / f_4(x)$. Second, in order to account for the seedlings/twigs showing little or no bud burst, the value of C_o was set at zero for chilling treatments in which fewer than a half of the buds showed bud burst:

$$C_o(x) = 0, \text{ when } BB\%(x) < 50\%$$

$$C_o(x) = \frac{f_4(\Delta t)}{f_4(x)}, \text{ when } BB\%(x) \geq 50\%$$

(17)

where C_o = ontogenetic competence, x = the duration of chilling, Δt = the duration of chilling required for rest completion, and $BB\%$ = bud burst percentage.

The value of ontogenetic competence, $C_o(t)$, was modelled with function f_3 by using the state of rest break, $S_r(t)$, as the argument in f_3 (Eqn. 5). In order to formulate function f_3 , the value of $S_r(x)$ was calculated for each duration of chilling x at a given constant chilling temperature as $100 x / \Delta t$. This simple formula is implied in the assumption that at any constant air temperature, rest break progresses at a constant rate (Eqn. 9).

Next, the values of $C_o(x)$ were plotted against $S_r(x)$ for all constant chilling temperatures used in the experiment, and a piece-wise linear equation was fitted to the scatter plot of the data points (see Figure 4 in the Results Section):

$$C_o(S_r) = 0, S_r < S_{r,min}$$

$$C_o(S_r) = a_3 S_r + b_3, S_r \geq S_{r,min}$$

(18)

347

348 where C_o = ontogenetic competence, S_r = the state of rest break, $S_{r,min}$ = the minimum value of S_r
 349 showing an above-zero value of C_o in the plot. The fitting was constrained by the assumption that
 350 the direct line crosses the point (100,1), since the value of $C_o(100) = 1$ by definition. After rest
 351 completion at $S_r(t) = 100\%$, Eqn. (18) was not applied any longer; instead, the value of $C_o = 1$ was
 352 retained for the remaining simulation period, which ended in the predicted bud burst.

353

354 **2.4 | Model tests with independent bud burst data**

355

356 **2.4.1 | Testing procedure**

357

358 For testing the models developed, three sets of independent bud burst observations were used.
 359 Starting on 23 November for each annual cycle, the model of each material category was run until it
 360 predicted bud burst to occur. Whenever hourly temperature data were not available, they were
 361 generated from the daily temperature indices as follows (Zohner et al., 2020):

362

363

$$364 \quad T_{hour} = \frac{(T_{max} - T_{min})}{2} \times \sin\left(\frac{\pi}{12} \times time_{day} - \frac{\pi}{2}\right) + \frac{(T_{max} + T_{min})}{2}$$

365

(19)

367

368 where T_{min} and T_{max} are the daily minimum and the daily maximum temperature, respectively, and
 369 $time_{day}$ = the hour of the day addressed. The predicted bud burst dates were then compared with the

observed ones.

2.4.2 | Predicted dormancy dynamics and a short-term independent test of the models

In order to examine the dynamics of rest break and ontogenetic development predicted by the models, we calculated the predicted state of rest break, S_r , ontogenetic competence, C_o , and the state of ontogenetic development, S_o , for the period of autumn 2018 to spring 2019 both in natural conditions on the Zhejiang A&F University campus and in natural conditions on a nearby *Torreya* tree plantation (Zhang et al., 2021a). The calculations were based on hourly air temperature records collected by iButtons (Model DS1912L, Embedded Data Systems Co., Ltd, KY, USA) at the two respective sites. In order to provide the first short-term test with independent data, the timing of leafout predicted by the models was compared with leafout observations made in natural conditions on the campus with seedlings of all four species. Similarly, the timing of the flowering predicted for adult *Torreya* was compared with corresponding observations in the *Torreya* plantation.

2.4.3 | Phenology records

The models were tested against independent observational phenological records from the Chinese National Ecology Science Data Center (www.cnern.org.cn, Table 3). Within this network, phenological observations are made and recorded routinely by the professionals at each station in accordance with unified observation guidelines (China Meteorological Administration, 1993). Similarly to our experimental work, we determined vegetative bud burst on the basis of leafout and then, for testing the models, selected the date corresponding to it from the database. In addition, the

phenological observations for *Torreya* flowering from Ren, Long, Zhou, Zhang, Zhou (2017) were used for independent model testing (Table 3). For the simulations, the daily T_{\min} and T_{\max} values were obtained from meteorological stations of the China National Meteorological Information Center (www.data.cma.cn) located near the phenological stations (Table 3). The values of T_{\min} and T_{\max} were converted into hourly temperatures by means of Eqn. (19). The tests for the three species other than *Torreya* were carried out with the model developed for seedlings because no models for adult trees had been developed for these species.

2.4.4 | Warming experiment

Lastly, the models were tested with independent bud burst data collected in a whole-tree chamber (WTC) warming experiment on the Zhejiang A&F University campus in autumn, winter and spring 2019 – 2020. In the experiment we applied a complete 3x3 random design with nine treatments combining three levels of both spring and winter warming: ambient temperature (A), ambient plus two degrees warming (A+2), and ambient plus four degrees warming (A+4). The winter and spring warming treatments were conducted from 10 November 2019 to 10 February 2020 and from 11 February 2020 until the observed bud burst, respectively. In each treatment we had eight replicated first-year seedlings of each of the four species. The seedlings had been raised like those used in the experiments carried out for model development (Zhang et al., 2021a). Three WTCs (E-Lotus Technology Co., Beijing, China) were used in the experiment, one for each temperature level applied.

The nine temperature treatments were realized by moving seedlings from chamber to chamber. For each species, 24 seedlings were put in each of the three WTCs at the beginning of the experiment

on 10 November 2019. On 11 February 2020, three sub-groups of eight seedlings were randomly sampled in each chamber. One sub-group remained in the same chamber and the other two were transferred, each into one of the WTCs representing the other two temperature levels. In this way, nine temperature treatments simulating the current climate and eight different cases of climatic warming were created. The air temperature records in each chamber were collected with iButtons (Model DS1912L, Embedded Data Systems Co., Ltd, KY, USA). Bud development was observed and the timing of bud burst was determined as they were in the experiments producing the experimental data for model development (Zhang et al., 2021a).

2.5 | Sensitivity analysis

In order to examine the potential role of temperatures below +5 °C in the rest break and the subsequent timing of bud burst, simulations of bud burst timing with long-term air temperature data as input were carried out with two models for each of the five material categories. In addition to the original model, we applied a modified model that assumed the rate of rest break to be at the maximum at any air temperature below +5 °C (see Figure 2 in the Results Section). We made use of the daily temperature records from Hangzhou, southeastern China (30°08'N, 120°06'E) for 1958 – 2018 by converting them into hourly temperatures by means of Eqn. (19).

2.6 | Scenario simulations

The effects of climatic warming on the spring phenology were assessed by projecting the timing of bud burst for 2020 – 2099 by means of the NASA Earth Exchange Global Daily Downscaled Climate Projections (NASA NEX-GDDP) data set. This data set is comprised of downscaled

climate scenarios for the globe that are derived from the General Circulation Model (GCM) runs conducted under the Coupled Model Intercomparison Project Phase 5 (CMIP5, Taylor, Ronald, & Meehl, 2011). We used daily minimum and maximum temperature records with a spatial resolution of $0.5 \times 0.5^\circ$ under two climatic scenarios, RCP 4.5 and RCP 8.5, (Meinshausen et al., 2011), which represented warming by 1.4 and 4.8 °C, respectively, for the period of 2020 – 2100 at our research site (Hangzhou). These data have been bias-corrected (Thrasher, Maurer, McKellar, & Duffy, 2012). The daily temperature records were converted into hourly temperatures by means of Eqn. (19). The predicted yearly times of leafout / flowering were plotted against time and, in order to quantify the effects of warming, a linear regression was fitted to the data.

2.7 | The software used in the study

Most of the data analyses and model calculations were carried out with R statistical software v.4.0.2 (R Development Core Team, 2020). The sensitivity analyses were done with source codes written in Fortran with the Visual Studio 2010 software.

3 | Results

3.1 Process-based models for the five material categories

Sub-model I

For *Torreya* trees, the experimental results show a clear decrease in the rate of rest break at temperatures upwards of +5 °C (Figure 2e; Table 4). A basically similar decrease was also found for *Pseudolarix* and *Torreya* seedlings, but because the decrease was less steep in these two material categories, their model formulation required extrapolation for temperatures above +15 °C (Section 2.3.2; Figure 2c,d; Table 4). In *Castanopsis* seedlings, a plateau response over the measured

temperature range was found, and accordingly, a horizontal line was used in the curve fitting for the model formulation (Figure 2a; Table 4). A similar plateau response was also assumed for *Phoebe* seedlings, despite an outlier observed at +15 °C (Figure 2b; Table 4). For both *Castanopsis* and *Phoebe* seedlings, extrapolation was needed at temperatures above +15 °C (Figure 2a,b; Table 4). For temperatures below +5 °C, extrapolation was needed with all five material categories. For this low-temperature end, two optional responses were formulated for each material category (Figure 2; Table 4). The maximal rate of rest break was relatively low in *Castanopsis* seedlings (Figure 1a), high in *Phoebe* seedlings (Figure 2b) and *Torreya* trees (Figure 2e), and intermediate in *Pseudolarix* (Figure 2c) and *Torreya* (Figure 2d) seedlings.

478

479 *Sub-model II*

For the air temperature response of the potential rate of ontogenetic development, $R_{o,pot}$, the sigmoidal equation fitted to the results for all five material categories quite well in general (Figure 3; Table 5). At high temperatures, however, there was a great deal of variation in the $R_{o,pot}$ values among the *Castanopsis* (Figure 3a) and *Pseudolarix* (Figure 3c) seedlings. In the estimated air temperature response of $R_{o,pot}$, there were marked differences among the material categories (Figure S3). For *Castanopsis*, *Phoebe*, and *Torreya* seedlings, the lower temperature threshold for ontogenetic development was estimated to be approximately +10 °C, whereas for *Torreya* trees and *Pseudolarix* seedlings, the rate of ontogenetic development was estimated to be considerable at temperatures below +10 °C also (Figure 3, Figure S3). For *Torreya* seedlings, the curve was estimated to level off at +20 °C already, and their rate of development was also estimated to be generally lower than that of the other material categories (Figure 3, Figure S3). For *Castanopsis*, *Phoebe*, and *Pseudolarix* seedlings, the curve levelled off near +30 °C, whereas for *Torreya* trees, no levelling off was found (Figure 3, Figure S3).

493

494 *Sub-model III*

495 Considerable differences were found among the material categories in the estimated dependence of
 496 ontogenetic competence, C_o , on the state of rest break, S_r (Figure 4; Table 6). In broad terms, three
 497 patterns are seen in the results. First, in *Torreya* trees, C_o stays at zero until S_r reaches about 68 %,
 498 after which C_o abruptly attains its near-maximal value (Figure 4e). Second, similarly to *Torreya*
 499 trees, in *Pseudolarix* (Figure 4c) and *Torreya* (Figure 4d) seedlings, C_o stays at zero with low values
 500 of S_r , but in contrast to *Torreya* trees, C_o gets positive values as soon as S_r reaches about 25 %. After
 501 that, C_o increases with increasing values of S_r in these two material categories. Third, in
 502 *Castanopsis* (Figure 4a) and *Phoebe* (Figure 4b) seedlings, C_o has a positive value even at $S_r = 0$ %,
 503 indicating that in these two species leafout can take place even without chilling. Considerable
 504 differences among the five material categories were also found in the slope of the dependence of C_o
 505 on S_r (Figure 4; Table 6).

506

507 **3.2 | Tests of the models with independent bud burst data**

508

509 **3.2.1 | Predicted dormancy dynamics and a test with short-term phenology records**

510 The dormancy dynamics implied by the ecophysiological phenomena addressed by the three sub-
 511 models are relatively complicated, giving rise to predictions that often cannot be discovered, not
 512 even in qualitative terms, without computer simulations. These dynamics are illustrated in Figure 5
 513 for the five material categories addressed in the present study.

514

515 For all five material categories, rest break was predicted to start at the beginning of the simulation
 516 on November 23, as indicated by the increasing values of the state of rest break, S_r (Figure 5b-f).
 517 This was because at the time, the air temperature was mainly fluctuating in the rest-breaking range

518 already (Figure 5a; compare with Figure 2). Rest break was the fastest in *Phoebe* seedlings, where
 519 rest completion was predicted to occur on 27 December (Figure 5c). This is because *Phoebe*
 520 seedlings retain their high rate of rest break over a broad temperature range (Figure 2b). In the other
 521 material categories, rest completion varied from 8 January in *Torreya* trees (Figure 5f) to 13
 522 February in *Castanopsis* seedlings (Figure 5b).

523

524 Besides the predicted S_r , the rate of ontogenetic development is also affected by two other
 525 phenomena. First, there are differences among the material categories in the dependence of
 526 ontogenetic competence, C_o , on S_r (Sub-model III; Figure 4); thus *Torreya* seedlings, for instance,
 527 started their ontogenetic development earlier (with $S_r = 24.85\%$, Figure 4d) than *Torreya* trees (with
 528 $S_r = 67.29\%$, Figure 4e), even though no major differences in rest break (development of S_r) were
 529 seen between them (Figure 5e,f). Second, even when two material categories have the same C_o ,
 530 there may be differences in their rate of ontogenetic development (Sub-model II, Figure 3, Figure
 531 S3). *Torreya* seedlings, for instance, show an exceptionally low rate of ontogenetic development
 532 (Figure S3), and accordingly, despite their earlier start of ontogenetic development, the *Torreya*
 533 seedlings showed predicted bud burst later than the *Torreya* trees showed predicted flowering
 534 (Figure 5e,f).

535

536 In predicting the timing of spring phenology, the highest accuracy was reached with *Pseudolarix*
 537 seedlings, where the prediction was one day late (Figure 5d). *Pseudolarix* seedlings were followed
 538 by *Phoebe* seedlings (two days early, Figure 5c), *Castanopsis* seedlings (seven days late, Figure 5b),
 539 *Torreya* trees (seven days early, Figure 5f), and *Torreya* seedlings (fifteen days late, Figure 5e).

540

541

542 3.2.2 | Independent tests with phenology records and results of the warming experiment

The models developed for *Torreya* provided relatively accurate predictions for both the timing of flowering in the observational phenological records and the timing of seedling leafout found in the warming WTC experiment of the present study (Figure 6d). For *Torreya*, the predictions were also unbiased.

For the other three species, no model for adult trees was developed in the present study, so that for predicting the timing of leafout in adult trees documented in the phenological records, the seedling leafout model was used. In comparison with *Torreya*, the accuracy reached with the other three species was lower (Figure 6a,b,c). Additionally, a bias was introduced into the model predictions for *Phoebe* (Figure 6b) and *Pseudolarix* (Figure 6c) as the model predictions were systematically earlier than the observations. No clear accuracy difference between the predictions of leafout for adult trees and leafout for seedlings (phenology records vs. warming experiment, Figure 6a,b,c) was found in any of these three species.

3.3 | Sensitivity analysis

In the sensitivity analysis of the role that temperatures below +5 °C in rest break may have on the timing of the subsequent bud burst, considerable differences were found among the five material categories (Table 7). In *Torreya*, *Phoebe*, and *Castanopsis* seedlings, a negligible sensitivity to the difference represented by the two alternative models used as Sub-model I was found. The percentage of the years with a difference in the timing of bud burst found between the two alternative sub-models in *Torreya*, *Phoebe*, and *Castanopsis* seedlings was 1.6 %, 6.6 %, and 19.7 % respectively, but in all years where there was a difference, the modified model predicted bud

burst to occur only one day earlier than the original model (Table 7). *Pseudolarix* seedlings displayed an intermediate sensitivity, with a difference between the predictions of the alternative models appearing in 77 % of the years. Between the results obtained with the two alternative sub-models, the average difference was 1.9 days and the maximum difference 7 days. *Torreya* trees showed the highest sensitivity, with a difference between the two simulations in almost all years, with the average and maximal differences of 2.5 and 17 days respectively, between the results obtained with the two alternative sub-models (Table 7).

3.4 | Scenario analyses

The timing of spring phenology was projected to advance in all scenario simulations that addressed the effects of climatic warming in 2020 – 2100 (Figure 7, Figure S4). Among the seedlings of the four species, the advances in the rates of leafout varied between 0.4 and 0.8 days per decade for RCP4.5 and between 2.8 and 3.5 days per decade for RCP8.5. The projected advances in seedling leafout per one °C warming varied between 4.7 and 5.9 days per °C, with no major differences between the two climatic scenarios (Figure 7a,b,c,d). For *Torreya* flowering, the results were different from those for leafout in the seedlings: first, a relatively minor advance of 0.4 and 0.9 days per decade was projected for RCP4.5 and RCP8.5, respectively. Second, there was a major difference between the advances per °C warming projected for RCP4.5 (2.3 days per °C) and for RCP8.5 (0.9 days per °C) (Figure 7e).

4 | DISCUSSION

4.1 | Biological realism of the models

We introduced novel process-based models of spring phenology for four subtropical tree species. The main emphasis in our modelling was on the biological realism of the models (Levins, 1966,

1968; Charrier, Ngao, Saudreau, & Améglio, 2015; Hänninen, 2016), which is why we took an experimental approach explicitly addressing the ecophysiological phenomena modelled. This approach, referred to as *the ecophysiological approach* by Hänninen (2016), has been taken with boreal and temperate trees only rarely (Sarvas, 1972, 1974; Campbell & Sugano, 1975, 1979; Caffarra, Donnelly, & Chuine, 2011) and, to our knowledge, with subtropical trees never before. The obvious reason for the shortage of earlier studies is the large amount of labour required by the experiments. The modular model structure adopted in the present study (Figure 1) facilitates the designing of particular experiments with each one addressing a specific ecophysiological phenomenon that affects the timing of the spring phenological event. The modular model structure was introduced as early as 30 years ago, but as far as we know, our study is the first one where it was used to its full potential, basing all three submodels on specific experimental data for the species addressed.

In the process-based modelling of tree spring phenology, an approach partially based on previous experimental findings is sometimes taken. In this approach, referred to as *the intermediate approach* by Hänninen (2016), rest break is simulated by accumulating chilling units and ontogenetic development by accumulating forcing units, with both based on temperature responses previously determined experimentally for some other species than the ones being modelled. In that approach, only the chilling and forcing requirements are determined on the basis of species-specific data (Häkkinen, Linkosalo, & Hari, 1998; Luedeling, Zhang, McGranahan, & Leslie, 2009; Xu, Dai, Ge, Wang, & Tao, 2020). With reference to the temperature responses determined in the present study (Figures 2, 3), this would mean that the shape of the temperature response curve is fixed *a priori* but the level is estimated from new species-specific data: the higher the chilling/forcing requirement, the lower the level of the corresponding curve (Hänninen, 2016).

618 Our explicit experimental results show that there are considerable differences among the examined
 619 four subtropical tree species in their air temperature responses of the rate of rest break (Figure 2)
 620 and ontogenetic development (Figure 3). Similar differences were found between the two life stages
 621 of *Torreya* addressed (Figures 2e,f, 3e,f). Even bigger differences were found between our results
 622 for the subtropical trees and those found earlier for boreal and temperate trees. Most importantly,
 623 we found that temperatures of up to +15 °C are effective in the rest break of many subtropical tree
 624 species. In fact, with the exception of adult *Torreya* trees, we were not even able to determine the
 625 upper limit of the rest-breaking temperature range for the subtropical tree species we studied (Zhang
 626 et al., 2021a). In most of the previous experimental studies of more northern trees, the upper
 627 threshold was found to be +10 to +12 °C or lower (Sarvas, 1974; Heide & Prestrud, 2005, however,
 628 see Erez & Couvillon, 1987). Similarly, we found in the present study that temperatures between 0
 629 and +10 °C, which have been found to promote ontogenetic development towards bud burst in
 630 boreal and temperate trees (Sarvas, 1972), are ineffective for many subtropical trees. All of these
 631 comparisons indicate that there is no chilling unit for rest break and no forcing unit for ontogenetic
 632 development based on response curves fixed *a priori* that could be universally valid for all species.
 633 Rather, the modelling needs to be based on species-specific or possibly even on provenance-specific
 634 data (Hänninen, 2016).

635

636 In seeking to attain species-specific models, an approach referred to as *the phenological approach*
 637 by Hänninen (2016) is often taken. In this approach, process-based tree phenology models are
 638 developed with the technique of inverse modelling, which means that rather than basing the models
 639 and their parameter values on experimental studies explicitly designed to examine the processes
 640 involved, the models and their parameter values are determined by fitting the models statistically to
 641 observational long-term phenological records (Kramer, 1994; Chuine, Cour, & Rousseau, 1998,
 642 Basler, 2016). The approach has become popular as it requires no experimental work and as long-

term phenological records are nowadays readily available for several tree species and geographical locations. Accordingly, when developing the first process-based model for a subtropical tree species, Chen et al. (2017), too, took the observational approach by using inverse modelling. However, as already shown by the pioneering study of Hunter and Lechowicz (1992), inverse modelling involves an exceptionally high degree of uncertainty. It often produces biologically unrealistic models, such as the ones suggesting that temperatures above 100 °C belong to the chilling temperature range (Kramer, 1994; for a recent discussion of the problems related to inverse modelling, see Hänninen et al., 2019). Unfortunately, the study of Chen et al. (2017), too, was undermined by unrealistic temperature responses of chilling accumulation (Figure S5).

4.2 | Further model development

In the sub-model for the air temperature response of the rate of rest break, extrapolation was generally needed at both the low and the high end of the temperature spectrum, so that experiments with temperatures in these temperature ranges are needed. Other aspects to be addressed in future modelling work include the effects of fluctuating temperatures (Fishman, Erez & Couvillon, 1987a,b) and of photoperiod (Zhang et al., 2021b) on rest break. Yet another aspect to be addressed is the changes that may occur during dormancy in the range of temperatures that promote ontogenetic development (Vegis, 1964; Junttila & Hänninen, 2012; Lundell, Hänninen, Saarinen, Åström & Zhang, 2020).

4.3 | Projected effects of climatic warming

In our scenario analyses, an advancing of the spring phenology was projected for all five material categories addressed (Figure 7). For the seedlings of the four species, the projected advancing per

one °C warming varied between 4.7 and 5.9 days per °C, which is in line with the corresponding projections obtained in earlier studies for temperate tree species (Kramer, 1994; Murray et al., 1994; Wang et al., 2020). For *Torreya* flowering, however, a smaller advancing was projected, and the advancing per one °C warming was much less for RCP8.5 than for RCP4.5 (Figure 7). In accordance with our hypothesis, the deviating results projected for *Torreya* flowering are explained by the peculiar aspects of the dormancy processes in *Torreya* flower buds, which are different from the corresponding processes in the vegetative buds of the seedlings of the four species studied.

First, rest break in *Torreya* trees proceeds relatively slowly at +10 °C, and at temperatures above +15 °C, no rest break is seen (Figure 2d). In the future, then, an increasing part of the winter will be too warm for rest break in *Torreya* flower buds, setting *Torreya* trees apart from the seedlings of the four species, especially those of *Castanopsis* and *Phoebe*. Second, rest break in *Torreya* trees needs to progress into an exceptionally late phase before any ontogenetic development is seen (Figure 4). This amplifies the effect of reduced chilling on its springtime phenology. Third, in comparison with the seedlings of the four species, the rate of ontogenetic development in *Torreya* trees shows a smaller increase in the temperature range of +10 to +20 °C (Figure S3), which is critical under climatic warming.

The deviating response of *Torreya* tree flowering to warming shows once again that process-based models should be based on specific responses determined by means of experiments explicitly designed to determine the responses of different species, also in different life stages of the given species. No modelling based on temperature responses fixed *a priori* could have revealed the deviating response to warming found for *Torreya* flowering.

4.4 Concluding remarks

693 We developed process-based models of spring phenology for four subtropical tree species. The
 694 development of the models was based entirely on specific experiments designed to address the
 695 processes, one at a time, that affect the spring phenology. Mostly, reasonable accuracy was attained
 696 in testing the models with independent data, both observational and experimental. In the application
 697 of the models to scenario simulations addressing the effects of climatic warming, an advancing of
 698 spring phenology was projected. Much less advancing was projected for flowering in *Torreya* than
 699 for leafout in the seedlings of the four species studied, and this was particularly the case under
 700 pronounced climatic warming. This difference was explained with reference to the peculiar
 701 dormancy processes typical for the flower buds of *Torreya* trees that were revealed in the
 702 experimentally based modelling. This shows the power of the experimental approach and, at the
 703 same time, calls for further experimental studies, our study being the first of its kind with
 704 subtropical trees.

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715 **CONFLICT OF INTEREST**

716 The authors declare no conflict of interest.

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AUTHOR CONTRIBUTION

R.Z., J.W. and H.H. designed the study. J.L., F.W. and R.Z. carried out the experiments. J.L., R.Z. and H.H. analyzed the data and carried out the modelling. R.Z., H.H. and J.L. wrote the study with inputs from J.W.

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964 **SUPPORTING INFORMATION**

965 Additional supporting information may be found online in the Supporting Information section at the

966 end of this article

968 TABLES

969 **TABLE 1** Experimental temperatures applied in the Spring experiments of 2018 – 2020 for
 970 formulating Sub-model II for each of the five material categories addressed in the study (seedlings
 971 of three species and both seedlings and twigs representing adult trees of *Torreya*)

972

Year	Experimental temperature
2018	+10 °C
	+17 °C
	+24 °C
2019	+12 °C
	+20 °C
	+28 °C
2020	+10 °C
	+15 °C
	+20 °C
	+25 °C

973

974 **TABLE 2** Duration of chilling, Δt , required at the experimental chilling temperatures for rest
 975 completion in the five material categories studied (seedlings of three species and both seedlings and
 976 twigs representing adult trees of *Torreya*). The values of Δt are indicated both in hours, as used in
 977 the modelling (Eqns. (1), (9); Table 4), and in days, as used in the plots to determine the values
 978 (Figures S1, Figure S2). No bud burst was observed in *Torreya* twigs after chilling at +15 °C

Material category	Chilling temperature	Δt , days	Δt , hours
<i>Castanopsis</i> seedlings	+5 °C	68.70	1649
	+10 °C	68.95	1655
	+15 °C	56.25	1350
<i>Phoebe</i> seedlings	+5 °C	33.72	809
	+10 °C	33.85	812
	+15 °C	19.34	464
<i>Pseudolarix</i> seedlings	+5 °C	52.70	1265
	+10 °C	69.45	1667
	+15 °C	102.81	2467
<i>Torreya</i> seedlings	+5 °C	26.31	631
	+6 °C	56.33	1352

	+10 °C	37.56	901
	+15 °C	69.51	1668
<i>Torreya trees</i>	+5 °C	31.21	749
	+6 °C	25.20	605
	+10 °C	56.00	1344
	+15 °C	-	-

979

980

981

982 **TABLE 3** The stations where phenological records were collected and the corresponding meteorological stations that provided air temperature
 983 data; both data sets were used in the present study for independent testing of process-based tree phenology models. For *Torreya*, the phenological
 984 data comprised female flowering (Station 4, Ren et al., 2019); for all other species, the phenological data comprised the leafout of vegetative
 985 buds in adult trees (Stations 1-3, Chinese National Ecology Science Data Center, www.cnern.org.cn). All temperature data were provided by the
 986 China National Meteorological Information Center (www.data.cma.cn)

Station index	Phenological station			Meteorological station			Years	Tree species
1	Changsha	28°06' N	113°00' E	Changsha	28°07' N	113°00' E	2005-2008	<i>Castanopsis</i> <i>Phoebe</i> <i>Pseudolarix</i>
2	Yinxian	29°36' N	121°12' E	Yinxian	29°31' N	121°20' E	1984-1996	<i>Pseudolarix</i>
3	Guilin	25°13' N	110°15' E	Guilin	25°09' N	110°06' E	2005, 2006, 2008	<i>Pseudolarix</i>
4	Guiyang	26°34' N	106°42' E	Guiyang	26°21' N	106°26' E	2014-2016	<i>Torreya</i>

987 **TABLE 4** Equations of Sub-model I for the five material categories studied (seedlings of three
 988 species and both seedlings and twigs representing adult trees of *Torreya*). Sub-model I represents
 989 the air temperature response of the rate of rest break, R_r (function f_1 in Eqn. 1 of the overall model;
 990 see Figure 2). In the modified model for each material category, the equations for all temperatures T
 991 $< +5$ °C are replaced by a constant value of R_r (dashed lines in Figure 2), either by using the
 992 constant value indicated by the shading (*Castanopsis* and *Phoebe* seedlings) or by calculating the
 993 constant value with the shaded equation with $T = +5$ °C (*Pseudolarix* and *Torreya* seedlings and
 994 *Torreya* trees)

Material category	Sub-model I: R_r (% h ⁻¹) =	
	0,	$T < -3.4$ °C
	$0.0077 T + 0.0263$,	-3.4 °C $\leq T < +5$ °C
<i>Castanopsis</i> seedlings	0.0650,	$+5$ °C $\leq T < +15$ °C
	$-0.0130 T + 0.2600$,	$+15$ °C $\leq T < +20$ °C
	0,	$T \geq +20$ °C
	0,	$T < -3.4$ °C
	$0.0183 T + 0.0623$,	-3.4 °C $\leq T < +5$ °C
<i>Phoebe</i> seedlings	0.1540,	$+5$ °C $\leq T < +15$ °C
	$-0.0308 T + 0.6160$,	$+15$ °C $\leq T < +20$ °C
	0,	$T \geq +20$ °C
<i>Pseudolarix</i> seedlings	0,	$T < -3.4$ °C

Material category	Sub-model I: R_r (% h ⁻¹) =
	$0.0094 T + 0.0319,$ $-3.4\text{ }^{\circ}\text{C} \leq T < +5\text{ }^{\circ}\text{C}$ $-0.0039 T + 0.0984,$ $+5\text{ }^{\circ}\text{C} \leq T < +15\text{ }^{\circ}\text{C}$ $-0.0080 T + 0.1596,$ $+15\text{ }^{\circ}\text{C} \leq T < +20\text{ }^{\circ}\text{C}$ $0,$ $T \geq +20\text{ }^{\circ}\text{C}$ $0,$ $T < -3.4\text{ }^{\circ}\text{C}$ $0.0150 T + 0.0509,$ $-3.4\text{ }^{\circ}\text{C} \leq T < +5\text{ }^{\circ}\text{C}$ $-0.0062 T + 0.1567,$ $+5\text{ }^{\circ}\text{C} \leq T < +15\text{ }^{\circ}\text{C}$ $-0.0127 T + 0.2548,$ $+15\text{ }^{\circ}\text{C} \leq T < +20\text{ }^{\circ}\text{C}$ $0,$ $T \geq +20\text{ }^{\circ}\text{C}$ $0,$ $T < -3.4\text{ }^{\circ}\text{C}$ $0.0185 T + 0.0627,$ $-3.4\text{ }^{\circ}\text{C} \leq T < +5\text{ }^{\circ}\text{C}$ $-0.0154 T + 0.2320,$ $+5\text{ }^{\circ}\text{C} \leq T < +15.1\text{ }^{\circ}\text{C}$ $0,$ $T \geq +15.1\text{ }^{\circ}\text{C}$
<i>Torreya</i> seedlings	
<i>Torreya</i> trees	

995 **TABLE 5** Parameter values of Sub-model II for the five material categories studied (seedlings of
 996 three species and both seedlings and twigs representing adult trees of *Torreya*). Sub-model II
 997 represents the sigmoidal air temperature response of the potential rate of ontogenetic development,
 998 $R_{o,pot}$ (function f_2 in Eqn. 4 of the overall model; see Figure 3). The potential rate of ontogenetic
 999 development indicates the rate after rest completion, when there is no longer any reduction of the
 1000 rate caused by the rest status of the bud. The parameters a_2 , b_2 , and c_2 indicate the upper asymptote
 1001 (maximal rate), steepness, and inflexion point of the sigmoidal curve, respectively

1002

Material category	a_2 (% h ⁻¹)	b_2 (°C ⁻¹)	c_2 (°C)	R^2
<i>Castanopsis</i> seedlings	0.3984	-2.9868	20.0907	0.8518
<i>Phoebe</i> seedlings	0.3451	-3.6026	20.5672	0.9041
<i>Pseudolarix</i> seedlings	0.3008	-3.6984	14.4639	0.6125
<i>Torreya</i> seedlings	0.1130	-1.8091	17.2439	0.9401
<i>Torreya</i> trees	0.2709	-8.8756	21.3366	0.8742

1003 **TABLE 6** Parameter values of Sub-model III (Eqn. 18) for the five material categories studied
 1004 (seedlings of three species and both seedlings and twigs representing adult trees of *Torreya*). Sub-
 1005 model III mediates the effect of the rest status on the rate of ontogenetic development towards bud
 1006 burst (Figure 1) by formulating the dependence of ontogenetic development, C_o , on the state of rest
 1007 break, S_r (function f_3 in Eqn. 5 of the overall model; see Figure 4)

Material category	Parameter		
	a_3	b_3	$S_{r,min}$
<i>Castanopsis</i> seedlings	0.0076	0.2410	0
<i>Phoebe</i> seedlings	0.0037	0.6334	0
<i>Pseudolarix</i> seedlings	0.0082	0.1765	20.16
<i>Torreya</i> seedlings	0.0044	0.5593	24.85
<i>Torreya</i> trees	0.0050	0.4974	67.29

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1009

TABLE 7 Results of the sensitivity analysis of the potential rest-breaking effects of temperatures below +5 °C on the timing of bud burst in the subsequent spring. The timing of bud burst in Hangzhou, southeastern China, was simulated for 61 years by using two alternative models for the temperature response of rest break. In the original model, no rest was assumed to take place at temperatures below -3.4 °C, whereas in the modified model, rest break was assumed to progress at its maximal rate at all temperatures below +5 °C (Figure 2; Table 4). The results in the table are for the years when there was a difference in the prediction between the two models. The positive values of the difference indicate that the modified model predicted an earlier bud burst than the original model

Material category	Percentage of years with a difference in the prediction	Mean difference (days)	Maximal difference (days)
<i>Castanopsis</i> seedlings	19.7	1	1
<i>Phoebe</i> seedlings	6.6	1	1
<i>Pseudolarix</i> seedlings	77.0	1.9	7
<i>Torreya</i> seedlings	1.6	1	1
<i>Torreya</i> trees	96.7	2.5	17

1022 FIGURE LEGENDS

1023 **FIGURE 1** The modular model structure applied in the present study for process-based modelling
 1024 of bud burst phenology in four subtropical tree species (Hänninen, 1990, 2016; Hänninen &
 1025 Kramer, 2007). The overall model consists of three sub-models, each one addressing the
 1026 corresponding particular ecophysiological phenomenon that affects the timing of bud burst. The red
 1027 font indicates the general structure of the overall model and the blue font the specific models
 1028 formulated in the present study on the basis of experimental data. In the present study, the model
 1029 was applied with a time step of one hour, using the hourly air temperature as input in the
 1030 simulations. Modified from Hänninen (2016)

1031 **FIGURE 2** Sub-model I for each of the five material categories examined, representing the
 1032 temperature response of the rate of rest break, R_r , (in the overall model, function f_1 in Eqn. 1). The
 1033 data points were determined on the basis of the experimental results of Zhang et al. (2021a). The
 1034 equations for f_1 are presented in Table 4. The value of the model variable R_r indicates how many per
 1035 cent of the physiological changes required for rest completion take place in one hour. The value R_r
 1036 $= 0.1 \text{ \% hour}^{-1}$, for instance, implies that 1000 hours are required at the particular temperature for
 1037 rest completion. The dotted lines indicate the modified model used in the sensitivity analysis that
 1038 addressed the uncertainty caused by the lack of data for temperatures under $+5 \text{ }^\circ\text{C}$

1039 **FIGURE 3** Sub-model II for each of the five material categories examined, representing the
 1040 temperature response of the potential rate of ontogenetic development, $R_{o,pot}$, (in the overall model,
 1041 function f_2 in Eqn. 4). Function f_2 is formulated according to Eqn. (16) with the parameter values
 1042 presented in Table 5. The potential rate of ontogenetic development indicates the rate at rest
 1043 completion, i.e., when the chilling requirement has been met and the rate is no longer restricted by
 1044 the rest condition of the bud. More specifically, $R_{o,pot}$ indicates how many per cent of the
 1045 ontogenetic changes within the bud required for leafout/flowering take place after rest completion

1046 in one hour. The value $R_{o,pot} = 0.2 \text{ \% hour}^{-1}$, for instance, implies that at the particular temperature,
 1047 500 hours after rest completion are required for leafout/flowering

1048 **FIGURE 4** Sub-model IIII for each of the five material categories examined, representing the
 1049 dependency of ontogenetic competence, C_o , on the state of rest break, S_r , (in the overall model,
 1050 function f_3 in Eqn. 5). The data points were determined on the basis of the experimental results of
 1051 Zhang et al. (2021a). Function f_3 is formulated according to Eqn. (18) with the parameter values
 1052 presented in Table 6. The value of S_r indicates the percentage of the physiological changes of rest
 1053 break caused by chilling and required for rest completion that have taken place at a given moment.
 1054 The value of C_o indicates the relative effect of the rest condition on the rate of ontogenetic
 1055 development. With $C_o = 0.5$, for instance, twice as much time is required for leafout/flowering as is
 1056 required after rest completion ($S_r = 100 \text{ \%}$) with $C_o = 1$

1057 **FIGURE 5** (a) Daily mean temperatures for the campus seedling collection (for seedlings of the
 1058 four species in panels b-e) and for the *Torreya* tree plantation (for *Torreya* trees in panel f). (b-f)
 1059 Predicted dormancy dynamics for autumn 2018 and spring 2019 of the five material categories
 1060 addressed in the study. The vertical axis on the left represents the state of rest break, S_r , (blue line)
 1061 and the state of ontogenetic development, S_o , (orange line). Rest completion is predicted to occur
 1062 when $S_r = 100 \text{ \%}$ (date marked in a blue font) and leafout/flowering when $S_o = 100 \text{ \%}$ (date marked
 1063 in an orange font). The observed leafout/flowering is marked with a circle and the date in a black
 1064 font. The vertical axis on the right represents ontogenetic competence, C_o , (red line). By definition,
 1065 $C_o = 1$ at rest completion, when $S_r = 100 \text{ \%}$. Otherwise the relationship between C_o and S_r varies
 1066 among the five material categories as shown in Figure 4

1067 **FIGURE 6** Independent tests of the process-based spring phenology models developed for the four
 1068 subtropical tree species by using both phenological records and results from our warming whole-
 1069 tree chamber (WTC) experiment. The phenological records represent adult trees (flowering in
 1070 *Torreya*, leafout in the other three species), whereas the results from the WTC experiment represent

1071 leafout in the seedlings of all four species. The predictions for the phenological records of
1072 *Castanopsis*, *Phoebe*, and *Pseudolarix* trees were calculated by means of the models developed for
1073 seedlings because no model for adult trees had been developed for these species in the present study

1074 **FIGURE 7** Projected timing of spring phenology (flowering for *Torreya* trees, leafout for the
1075 seedlings of the four species) for 2020 – 2100 under the climatic scenarios RCP4.5 and RCP8.5.
1076 The projections were calculated by means of the process-based models developed in the present
1077 study. The trends are presented here with direct lines fitted to the results; for the original yearly
1078 results, see Figure S4