PRIMARY RESEARCH ARTICLE

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

Running title: Phenology in subtropical trees

Rui Zhang^{1,2,#} | Jianhong Lin^{1,#} | Fucheng Wang¹ | Heikki Hänninen^{1,2} | Jiasheng Wu^{1,2}

¹State Key Laboratory of Subtropical Silviculture, Zhejiang A&F University, 666 Wusu Street,
Hangzhou 31 1300, China; ²SFGA research center for *Torreya grandis*, Zhejiang A&F University,
666 Wusu Street, Hangzhou 31 1300

[#] R. Zhang and J. Lin are to be considered joint first authors.

Correspondence

Jiasheng Wu

wujs@zafu.edu.cn

Heikki Hänninen

hhannin@zafu.edu.cn

24 **Funding information**

25 The study was financed by The Chinese National Natural Science Foundation [31800579], The
26 National Forestry and Grassland Technological Innovation Program for Young TopNotch Talents
27 [2020132604], Zhejiang Provincial Natural Science Foundation of China [LQ18C160001], the Key
28 Research Program of Zhejiang Province [2018C02004], the Major Project for Agricultural Breeding
29 of Zhejiang Province [2016C02052-12], and Overseas Expertise Introduction Project for Discipline
30 Innovation (111 Project D18008).

31

Abstract

To project the effects of climatic warming on the timing of spring leafout and flowering in trees, process-based tree phenology models are often used nowadays. Unfortunately, the biological realism of the models is often compromised because the model development has often been based on various assumptions and indirect methods. We developed process-based tree phenology models for four subtropical tree species, and for the first time for these trees, we based the model development on explicit experimental work particularly designed to address the processes being modelled. For all the four species, a model of seedling leafout was developed, and for *Torreya grandis*, a model for female flowering in adult trees was additionally developed. The models generally showed reasonable accuracy when tested against two sources of independent data: observational phenological records and leafout data from a whole-tree chamber warming experiment. In scenario simulations, the models projected an advanced spring phenology under climatic warming for 2020 – 2100. For the leafout of seedlings, the advancing rates varied between 4.7 and 5.9 days per one °C warming, with no major differences found between the climatic scenarios RCP4.5 and RCP8.5. For *Torreya* flowering, less advancing was projected, and the projected advancing per one °C warming was less for RCP8.5 (0.9 days / °C) than for RCP4.5 (2.3 days / °C). The low advancing rates of *Torreya* flowering were caused by reduced chilling under the warming climate and by the particular temperature responses found for *Torreya* flowering. For instance, our results show that in *Torreya* flower buds, no rest break (endodormancy release) is seen at +15 °C, whereas in the seedlings of all four species, +15 °C has a clear rest-breaking effect. These findings highlight the need to base the model development on explicit experiments particularly designed to address the process being modelled.

57 **KEYWORDS**

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

60

1 | Introduction

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

After growth cessation in autumn, the buds of boreal and temperate trees attain the state of rest (endodormancy; Lang, Early, Martin, & Darnell, 1987), where bud burst and growth onset are prevented by physiological factors inside the buds (Perry, 1971; Fuchigami, Weiser, Kobayashi, Timmis, & Gusta, 1982; Hänninen & Tanino, 2011). The growth-arresting conditions are removed by prolonged (days to months) exposure to low chilling temperatures; traditionally, temperatures near +5 °C have been regarded as necessary for chilling (Sarvas, 1974). This is the chilling

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

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

110 of the projected climate change (Cannell, 1985; Hänninen, 1991; Kramer, 1994; Chuine et al.,
111 2016).

112

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

133

134 2 | MATERIALS AND METHODS

135 2.1 | Model structure

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

143

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

146

$$147 \quad R_r(T(t)) = f_1(T(t))$$

148 (1)

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

152

$$153 \quad S_r(t) = \int_{t_0}^t R_r(T(t)) dt$$

154 (2)

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

158

159

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

160

(3)

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

163 Sub-model II addresses the effects of high forcing temperatures on the rate of ontogenetic
 164 development after rest completion. That particular rate is called the potential rate of ontogenetic
 165 development, $R_{o,pot}$, because after rest completion the rate of ontogenetic development is no longer
 166 restricted by the rest condition. The momentary $R_{o,pot}$ is calculated as a function of air temperature,
 167 $T(t)$:

168

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

169

(4)

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

171

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

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

$$181 \quad C_o(t) = f_3(S_r(t))$$

182 (5)

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

$$186 \quad R_o(t) = C_o(t)R_{o,pot}(t)$$

187 (6)

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

$$190 \quad S_o(t) = \int_{t_0}^t R_o(T(t), C_o(t)) dt$$

191 (7)

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

$$195 \quad S_o(t) = 100 \%$$

196 (8)

197

198 **2.2 | Tree species and experimental data**

199 **2.2.1 | Material categories**

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

207

208 **2.2.2 | Autumn experiments for Sub-models I and III**

209 In the autumn experiments carried out in 2017 – 2019, the experimental seedlings and twigs were
 210 first subjected to chilling for periods of varying duration, then transferred to growth-promoting
 211 forcing conditions with a constant air temperature of +20 °C (Zhang et al., 2021). The chilling
 212 treatments were carried out in growth chambers at three constant temperatures: +5 °C, +10 °C, and
 213 +15 °C. In the forcing conditions, a regrowth test was carried out by observing the occurrence and
 214 timing of bud burst (leafout, flowering; see Section 2.2.3). For each observed seedling or twig
 215 showing bud burst, the days to bud burst in the forcing conditions, DBB, was calculated. For each
 216 treatment representing a given duration of chilling at a given chilling temperature, the value of bud
 217 burst percentage, BB%, was calculated.

218

219 **2.2.3 | Spring experiments for Sub-model II**

220 The effects of the air temperature on the potential rate of ontogenetic development were addressed
 221 in the three spring experiments, carried out in the years 2018 – 2020. Until the start of the
 222 experiment, the experimental seedlings and trees overwintered in natural conditions on the Zhejiang
 223 A&F University campus (30°14'N, 119°42'E) in Hangzhou, southeastern China. In order to make
 224 sure that the actual rate of ontogenetic development observed in the experiment represented the
 225 potential rate, the spring experiments of all the three years 2018 – 2020 were started on 13
 226 February, after all the material categories had met the chilling requirement in natural conditions
 227 (Zhang et al., 2021). In each year, we transferred ten replicated seedlings of each species from
 228 natural outdoor conditions to forcing growth chambers (E-Lotus Technology Co., Beijing, China)
 229 with several constant air temperatures ranging from 10 to 28 °C (Table 1). At the same time, twigs
 230 of adult *Torreya* trees were sampled on the campus and transferred to the forcing chambers. The
 231 twigs and seedlings were prepared for the experiments in the same way as in the autumn
 232 experiments (Zhang et al., 2021). In all the forcing chambers, day length was 12 h, PPFD 400 μmol
 233 $\text{m}^{-2} \text{s}^{-1}$, relative humidity 70-80 %, and concentration of CO_2 300-400 ppm. Temperature of the
 234 chambers was monitored with iButton (Model DS1912L, Embedded Data Systems Co., Ltd, KY,
 235 USA). Bud burst was observed visually, as had been done in the autumn experiments (Zhang et al.,
 236 2021). In the seedlings of all four species, the determination of bud burst was based on the stage of
 237 leafout, and in the *Torreya* twigs representing adult trees, on female flowering. Despite these
 238 differences, the term ‘bud burst’ is used in this report as a generic one in connection with the
 239 standard variables BB% and DBB (Zhang et al., 2021). For each experimental seedling and twig,
 240 the days to bud burst in the forcing conditions, DBB, was calculated.

241

242 **2.3 | Formulating the models on the basis of experimental data**

243 **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

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

288

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

291 The Δt values obtained (Table 2; Figure S2) were plugged into Eqn. (9), thus getting three (for
292 *Castanopsis*, *Phoebe*, and *Pseudolarix* seedlings) or four (for *Torreya* seedlings and twigs) data
293 points for R_r in the temperature range of +5 to +15 °C (see Figure 2 in the Results Section). In that
294 temperature range, the function f_l in Eqn. (1) was determined by fitting a direct line to the scatter
295 plot representing the observed R_r as a function of temperature. It was assumed that at temperatures
296 below +5 °C, R_r would drop from its maximum value (obtained at +5 °C) to zero at -3.4 °C (Sarvas,
297 1974). If extrapolation was also needed at the high temperature end, it was similarly assumed that
298 R_r would drop from its value at +15 °C to zero at +20 °C. In a sensitivity analysis addressing the
299 uncertainty caused by the lack of data for temperatures under +5 °C, a modified model was used. In
300 that model it is assumed that at any temperature below +5 °C, R_r has a constant value, identical to
301 the maximal value of R_r at +5 °C (see Figure 2 in the Results Section).

302

303 2.3.3 | Sub-model II

304 For Sub-model II, the potential rate of ontogenetic development at any constant temperature T' ,
305 $R_{o,pot}(T')$, was determined experimentally as follows (Sarvas, 1972; Campbell, 1978):

306

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

307

308 (15)

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

310 Because of the multiplier 100, the unit of $R_{o,pot}$ is $\% h^{-1}$, so that the value of $R_r(T')$ indicates how

311 many per cent of the ontogenetic changes required for bud burst take place within one hour.

312

313 The values of $R_{o,pot}(T')$ were plotted against the experimental temperature T' . The air temperature

314 response of $R_{o,pot}$ (function f_2 in Eqn. 4) was formulated by fitting a sigmoidal function to the scatter

315 plot (see Figure 3 in the Results Section):

$$316 \quad R_{o,pot}(T) = \frac{a_2}{1 + e^{\frac{1}{b_2}(T - c_2)}}$$

317

318 (16)

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

320

321 2.3.4 | Sub-model III

322 By the definition of ontogenetic competence, C_o , (Section 2.1, Eqn. 6), the empirical value of C_o for

323 a given seedling/twig is zero if it shows no bud burst during prolonged forcing, and by the same

324 token, it is unity if its DBB is equal to the DBB representing twigs and seedlings which have just

325 attained rest completion, i.e., equal to $DBB(\Delta t) = DBB_{RC}$ (Figure S1). Between these two extremes,

326 the value of C_o increases proportionally to the ratio of $DBB(\Delta t) / DBB$ of the seedling/twig. In the

327 calculation of the empirical values of C_o , two averaging methods were applied. First, the original

328 DBB observations of the individual twigs/seedlings were replaced by the fitted exponential

329 functions, f_4 (Eqn. 10; Figure S2). Accordingly, the value of C_o for any duration of chilling x at a

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

$$333 \quad C_o(x) = 0, \text{ when } BB\%(x) < 50 \%$$

$$334 \quad C_o(x) = \frac{f_4(\Delta t)}{f_4(x)}, \text{ when } BB\%(x) \geq 50 \%$$

$$335 \quad (17)$$

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

338

339 The value of ontogenetic competence, $C_o(t)$, was modelled with function f_3 by using the state of rest
340 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
341 calculated for each duration of chilling x at a given constant chilling temperature as $100 x/\Delta t$. This
342 simple formula is implied in the assumption that at any constant air temperature, rest break
343 progresses at a constant rate (Eqn. 9).

344

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

348

$$349 \quad C_o(S_r) = 0, \quad S_r < S_{r,min}$$

$$350 \quad C_o(S_r) = a_3 S_r + b_3, \quad S_r \geq S_{r,min}$$

(18)

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

2.4 | Model tests with independent bud burst data

2.4.1 | Testing procedure

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

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

(19)

where T_{min} and T_{max} are the daily minimum and the daily maximum temperature, respectively, and $time_{day}$ = 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., 2021). 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., 2021). 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., 2021).

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.

483

484 *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).

498

499 *Sub-model III*

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

511

512 **3.2 | Tests of the models with independent bud burst data**

513

514 **3.2.1 | Predicted dormancy dynamics and a test with short-term phenology records**

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

519

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

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

528

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

540

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

545

546

547 **3.2.2 | Independent tests with phenology records and results of the warming experiment**

548

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

553

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

562

563

564 **3.3 | Sensitivity analysis**

565

566 In the sensitivity analysis of the role that temperatures below +5 °C in rest break may have on the
567 timing of the subsequent bud burst, considerable differences were found among the five material
568 categories (Table 7). In *Torreya*, *Phoebe*, and *Castanopsis* seedlings, a negligible sensitivity to the
569 difference represented by the two alternative models used as Sub-model I was found. The
570 percentage of the years with a difference in the timing of bud burst found between the two
571 alternative sub-models in *Torreya*, *Phoebe*, and *Castanopsis* seedlings was 1.6 %, 6.6 %, and
572 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, erred 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). In a similar approach often taken, not even the shapes of the temperature response curves have any experimental basis. For instance,

623 the threshold chilling model, which assumes that one chilling unit is accumulated during each hour
624 when the air temperature is below a given threshold, is used quite frequently (Weinberger, 1950;
625 Cannell & Smith, 1983), but as far as we know, no explicit experimental data has been published to
626 document a response of that type.

627

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

645

646 In seeking to attain species-specific models, an approach referred to as *the phenological approach*
647 by Hänninen (2016) is often taken. In this approach, process-based tree phenology models are

developed with the technique of inverse modelling, which means that rather than basing the models and their parameter values on experimental studies explicitly designed to examine the processes involved, the models and their parameter values are determined by fitting the models statistically to observational long-term phenological records (Kramer, 1994; Chuine, Cour, & Rousseau, 1998, 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

Though our experimental approach explicitly addressed the processes being modelled, the models developed still require further work for better biological realism. Several additional aspects need to be addressed in further work of process-based modelling for subtropical trees. The most obvious one is seen in Figure 2, which shows that 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. However, when experiments are carried out to add the missing data points, various methodological problems are met. Temperatures above +15 °C generally cause ontogenetic development towards bud burst, thus lowering the value of DBB and confusing the determination of

the chilling duration required for rest completion. This problem can be addressed with computational techniques, such as simulated annealing (Chuine et al., 1998; Chuine, 2000; Lundell, Hänninen, Saarinen, Åström & Zhang, 2020). At the lower end of the temperature scale, problems may be met in chilling with freezing temperatures because subtropical tree species do not necessarily survive in continuous freezing conditions (Zhang et al., 2021). The sensitivity analyses of the present study also suggest that temperatures below +5 °C occur so rarely at the subtropical research site that their effect on rest break may be quite limited with most species. Still, at least the temperatures between zero and +5 °C need to be studied for their rest-breaking effects.

In addition, the effects of fluctuating temperatures (Fishman, Erez & Couvillon, 1987a,b) and of photoperiod on rest break (Zhang et al., 2020) need to be introduced into the process-based modelling for subtropical trees. Furthermore, the post-rest theory introduced by Vegis (1964) and recently formulated for boreal field layer plants by Lundell et al. (2020) should be examined with reference to subtropical trees, too. The theory suggests that the temperature range promoting ontogenetic development changes during dormancy. That change provides a potential explanation for the bias of the model prediction observed in the present study with two species in the independent test (Figure 6; Hänninen, 2016). The generic concept of ontogenetic competence (Figure 1) used in the present study was also used by Lundell et al. (2020), showing that the concept can be applied in a broad range of studies where restrictions caused by the rest status on the ontogenetic development need to be addressed.

Similarly to most studies of process-based tree phenology modelling, an indirect black-box modelling approach was taken in the present study, too, in that rather than considering the processes of rest break and ontogenetic development as such, only their final outcome (leafout, flowering) was observed in the experiments. For ontogenetic development, the processes could be addressed

by microscopic observations of the anatomical development of the bud (Sarvas 1972, 1974; Sutinen, Partanen, Viherä-Aarnio, & Häkkinen, 2012; Viherä-Aarnio, Sutinen, Partanen, & Häkkinen, 2014). This is because the models predict not only the occurrence of leafout/flowering when $S_o = 100\%$ but also the occurrence of a given anatomical stage of development when S_o attains a constant critical value ($< 100\%$) specific to the stage of development. Despite our improved understanding of the physiological mechanisms of rest and rest break (Rohde & Bhalerao, 2007; Cooke, Eriksson, & Junttila, 2012; Tylewicz et al., 2018), no corresponding markers have been available for similar testing of the models of rest break in regard to developmental events corresponding to S_r values below 100%. Chuine et al. (2016), however, suggested the use of the floral primordia fresh weight as such a marker for *Prunus armeniaca*. It would seem useful to examine that marker's suitability for other species as well.

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

We developed process-based models of spring phenology for four subtropical tree species. The development of the models was based entirely on specific experiments designed to address the processes, one at a time, that affect the spring phenology. Mostly, reasonable accuracy was attained in testing the models with independent data, both observational and experimental. In the application of the models to scenario simulations addressing the effects of climatic warming, an advancing of spring phenology was projected. Much less advancing was projected for flowering in *Torreya* than for leafout in the seedlings of the four species studied, and this was particularly the case under pronounced climatic warming. This difference was explained with reference to the peculiar dormancy processes typical for the flower buds of *Torreya* trees that were revealed in the

748 experimentally based modelling. This shows the power of the experimental approach and, at the
749 same time, calls for further experimental studies, our study being the first of its kind with
750 subtropical trees.

751

752 **ACKNOWLEDGEMENTS**

753 We thank Pekka Hirvonen (www.toisinsanoen.eu) for revising the language of the manuscript.

754

755 **CONFLICT OF INTEREST**

756 The authors declare no conflict of interest.

757

758 **AUTHOR CONTRIBUTION**

759 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
760 H.H. analyzed the data and carried out the modelling. R.Z., H.H. and J.L. wrote the study with inputs
761 from J.W.

762

763 **DATA AVAILABILITY STATEMENT**

764 The data that support the findings of this study are available from the corresponding author upon
765 reasonable request.

766

767 **ORCID**

768 *Heikki Hänninen* <https://orcid.org/0000-0003-3555-2297>

769 *Rui Zhang* <https://orcid.org/0000-0002-7235-505X>

770 *Jiasheng Wu* <https://orcid.org/0000-0002-2515-4677>

771

772 REFERENCES

- 773 Arnold, C.Y. (1959). The determination and significance of the base temperature in a linear heat
774 unit system. *Proceedings of the American Society of Horticultural Science*, 74, 430-445.
- 775 Basler, D. (2016). Evaluating phenological models for the prediction of leaf-out dates in six
776 temperate tree species across central Europe. *Agricultural and Forest Meteorology*, 217, 10-
777 21.
- 778 Caffarra, A., Donnelly, A., & Chuine, I. (2011). Modelling the timing of *Betula pubescens* budburst.
779 II. Integrating complex effects of photoperiod into process-based models. *Climate Research*,
780 46, 159–170.
- 781 Campbell, R.K. (1978). Regulation of bud-burst timing by temperature and photoregime during
782 dormancy. In: C.A. Hollis, & A.E. Squillace (Eds.), *Proceedings: Fifth North American*
783 *Forest Biology Workshop* (pp. 19-33). Gainesville: Forestry Department, University of
784 Florida.
- 785 Campbell, R.K., & Sugano, A.I. (1975). Phenology of bud burst in Douglas-fir related to
786 provenance, photoperiod, chilling, and flushing temperature. *Botanical Gazette*, 136, 290-
787 298.
- 788 Campbell, R. K., & Sugano, A. I. (1979). Genecology of bud-burst phenology in Douglas-fir:
789 response to flushing temperature and chilling. *Botanical Gazette*, 140, 223-231.
- 790 Cannell, M.G.R. (1985). Analysis of risks of frost damage to forest trees in Britain. In P.M.A.
791 Tigerstedt, P. Puttonen, & V. Koski (Eds.), *Crop physiology of forest trees* (pp. 153-166).
792 Helsinki: Helsinki University Press.
- 793 Cannell, M.G.R., & Smith, R.I. (1983). Thermal time, chill days and prediction of budburst in *Picea*
794 *sitchensis*. *Journal of Applied Ecology*, 20, 951-963.
- 795 Chamberlain, C.J., Cook B.I., de Cortazar-Atauri, I.G., & Wolkovich, E.M. (2019). Rethinking false
796 spring risk. *Global Change Biology*, 25, 2209-2220.

- 797 Charrier, G., Ngao, J., Saudreau, M., & Améglio, T. (2015). Effects of environmental factors and
798 management practices on microclimate, winter physiology, and frost resistance in trees.
799 *Frontiers in Plant Science*, 6, 259. <https://doi.org/10.3389/fpls.2015.00259>.
- 800 Chen, X., Wang, L., & Inouye, D. (2017). Delayed response of spring phenology to global warming
801 in subtropics and tropics. *Agricultural and Forest Meteorology*, 234, 222-235.
- 802 China Meteorological Administration. (1993). *Observation criterion of agricultural meteorology*
803 (pp. 139-140). Beijing: China Meteorological Press. (in Chinese).
- 804 Chuine, I. (2000). A unified model for budburst of trees. *Journal of Theoretical Biology*, 207, 337-
805 347.
- 806 Chuine, I. (2010). Why does phenology drive species distribution? *Philosophical Transactions of*
807 *The Royal Society. B.*, 365, 3149-3160.
- 808 Chuine, I., & Beaubien, E.G. (2001). Phenology is a major determinant of tree species range.
809 *Ecology Letters*, 4, 500-510.
- 810 Chuine, I., Cour, P., Rousseau, D.D. (1998). Fitting models predicting dates of flowering of
811 temperate-zone trees using simulated annealing. *Plant, Cell and Environment*, 21, 455-466.
- 812 Chuine, I., Bonhomme, M., Legave, J-M., de Cortázar-Atauri, I.G., Charrier, G., & Lacoïnte, A.
813 (2016). Can phenological models predict tree phenology accurately in the future? The
814 unrevealed hurdle of endodormancy break. *Global Change Biology*, 22, 3444-3460.
- 815 Chuine, I., de Cortázar-Atauri, I.G., Kramer, K., & Hänninen, H. (2013). Plant development
816 models. In M.D. Schwartz (Ed.), *Phenology: An Integrative Environmental Science, Second*
817 *Edition* (pp. 275-293). Dordrecht: Springer Science+Business Media B.V.
- 818 Cooke, J.E.K., Eriksson, M.E., & Junttila, O. (2012). The dynamic nature of bud dormancy in trees:
819 environmental control and molecular mechanisms. *Plant Cell and Environment*, 35, 1707-
820 1728.
- 821 Coville, F.V. (1920). The influence of cold in stimulating the growth of plants. *Journal of*

- 822 *Agricultural Research*, 20, 151-160.
- 823 Delpierre, N., Guillemot, J., Dufrêne, E., Cecchini, S. & Nicolas, M. (2017). Tree phenological
824 ranks repeat from year to year and correlate with growth in temperate deciduous forests.
825 *Agricultural and Forest Meteorology*, 234, 1-10.
- 826 Du, Y., Pan, Y., Ma, K. (2019). Moderate chilling requirement controls budburst for subtropical
827 species in China. *Agricultural and Forest Meteorology*, 278, 107693.
828 <https://doi.org/10.1016/j.agrformet.2019.107693>
- 829 Erez, A., & Couvillon, G.A. (1987). Characterization of the influence of moderate temperatures on
830 rest completion in peach. *Journal of the American Society for Horticultural Science*, 112,
831 677-680.
- 832 Fishman, S., Erez, A., & Couvillon, G.A. (1987a). The temperature dependence of dormancy
833 breaking in plants: mathematical analysis of a two-step model involving a cooperative
834 transition. *Journal of theoretical Biology*, 124, 473-483.
- 835 Fishman, S., Erez, A., & Couvillon, G.A. (1987b). The temperature dependence of dormancy
836 breaking in plants: computer simulation of processes studied under controlled temperatures.
837 *Journal of theoretical Biology*, 126, 309-321.
- 838 Ford, K.R., Harrington, C.A., Bansal, S., Gould, P.J., & St Clair, J.B. (2016). Will changes in
839 phenology track climate change? A study of growth initiation timing in coast Douglas-fir.
840 *Global Change Biology*, 22, 3712-3723.
- 841 Fu, Y.H., Zhao, H., Piao, S., Peaucelle, M., Peng, S., Zhou, G., ... Janssens, I.A. (2015a). Declining
842 global warming effects on the phenology of spring leaf unfolding. *Nature*, 526, 104-107.
- 843 Fu, Y.H., Piao, S., Vitasse, Y., Zhao, H., De Boeck, H.J., Liu, Q., ... Janssens, I.A. (2015b).
844 Increased heat requirement for leaf flushing in temperate woody species over 1980–2012:
845 effects of chilling, precipitation and insolation. *Global Change Biology*, 21, 2687-2697.
- 846 Fu, Y.H., Piao, S., Zhou, X., Geng, X., Hao, F., Vitasse, Y., & Janssens, I.A. (2019a). Short

- 847 photoperiod reduces the temperature sensitivity of leaf-out in saplings of *Fagus sylvatica* but
848 not in horse chestnut. *Global Change Biology*, 25, 1696-1703.
- 849 Fu, Y.H., Zhang, X., Piao, S., Hao, F., Geng, X., Vitasse, Y., ... & Janssens, I.A. (2019b). Daylength
850 helps temperate deciduous trees to leaf-out at the optimal time. *Global Change Biology*, 25,
851 2410-2418.
- 852 Fuchigami, L.H., Weiser, C.J., Kobayashi, K., Timmis, R., & Gusta, L.V. (1982). A degree growth
853 stage (°GS) model and cold acclimation in temperate woody plants. In P.H. Li, & A. Sakai
854 (Eds.), *Plant cold hardiness and freezing stress. Mechanisms and crop implications. Volume*
855 *2* (pp. 93-116). New York: Academic Press.
- 856 Häkkinen, R., Linkosalo, T., & Hari, P. (1998). Effects of dormancy and environmental factors on
857 timing of bud burst in *Betula pendula*. *Tree Physiology*, 18, 707-712.
- 858 Hänninen, H. (1990). Modelling bud dormancy release in trees from cool and temperate regions.
859 *Acta Forestalia Fennica*, 213, 1-47.
- 860 Hänninen, H. (1991). Does climatic warming increase the risk of frost damage in northern trees?
861 *Plant, Cell and Environment*, 14, 449-454.
- 862 Hänninen, H. (1995). Effects of climatic change on trees from cool and temperate regions: an
863 ecophysiological approach to modelling of bud burst phenology. *Canadian Journal of*
864 *Botany*, 73, 183-199.
- 865 Hänninen, H. (2016). *Boreal and temperate trees in a changing climate: Modelling the*
866 *ecophysiology of seasonality*. Dordrecht: Springer Science+Business Media.
- 867 Hänninen, H., & Kramer, K. (2007). A framework for modelling the annual cycle of trees in boreal
868 and temperate regions. *Silva Fennica*, 41, 167-205.
- 869 Hänninen, H., & Tanino, K. (2011). Tree seasonality in a warming climate. *Trends in Plant Science*
870 16, 412-416.
- 871 Hänninen, H., Kramer, K., Tanino, K., Zhang, R., Wu, J., & Fu, Y.H. (2019). Experiments are

- 872 necessary in process-based tree phenology modelling. *Trends in Plant Science*, 24, 199-209.
- 873 Harrington, C.A., Gould, P.J., & St.Clair, J.B. (2010). Modeling the effects of winter environment
874 on dormancy release of Douglas-fir. *Forest Ecology and Management*, 259, 798-808.
- 875 Heide, O.M., & Prestrud, A.K. (2005). Low temperature, but not photoperiod, controls growth
876 cessation and dormancy induction and release in apple and pear. *Tree Physiology*, 25, 109-
877 114.
- 878 Hunter, A.F., & Lechowicz, M.J. (1992). Predicting the timing of budburst in temperate trees.
879 *Journal of Applied Ecology*, 29, 597-604.
- 880 Keenan, T.F., Gray, J., Friedl, M.A., Toomey, M., Bohrer, G., Hollinger, D.Y., ... Richardson, A.D.
881 (2014). Net carbon uptake has increased through warming-induced changes in temperate
882 forest phenology. *Nature Climate Change*, 4, 598-604.
- 883 Kramer, K. (1994). A modelling analysis of the effects of climatic warming on the probability of
884 spring frost damage to tree species in The Netherlands and Germany. *Plant, Cell and*
885 *Environment*, 17, 367-377.
- 886 Kramer, K., & Hänninen, H. (2009). The annual cycle of development of trees and process-based
887 modelling of growth to scale up from the tree to the stand. In A. Noormets (Ed.), *Phenology*
888 *of ecosystem processes* (pp. 201-227). Springer Science+Business Media, LLC.
- 889 Landsberg, J.J. (1974). Apple fruit bud development and growth; analysis and an empirical model.
890 *Annals of Botany*, 38, 1013-1023.
- 891 Lang, G.A., Early, J.D., Martin, G.C., & Darnell, R.L. (1987). Endo-, para-, and ecodormancy:
892 physiological terminology and classification for dormancy research. *HortScience*, 22, 371-
893 377.
- 894 Levins, R. (1966). The strategy of model building in population biology. *American Scientist*, 54,
895 421-431.
- 896 Levins, R. (1968). *Evolution in changing environments. Some theoretical explorations*. Princeton,

- 897 New Jersey: Princeton University Press.
- 898 Luedeling, E. (2012). Climate change impacts on winter chill for temperate fruit and nut
899 production: A review. *Scientia Horticulturae*, 144, 218-229.
- 900 Luedeling, E., Zhang, M., McGranahan, G., & Leslie, C. (2009). Validation of winter chill models
901 using historic records of walnut phenology. *Agricultural and Forest Meteorology*, 149:
902 1854-1864.
- 903 Lundell, R., Hänninen, H., Saarinen, T., Åström, H., Zhang, R. (2020). Beyond rest and quiescence
904 (endodormancy and ecodormancy): A novel model for quantifying plant-environment
905 interaction in bud dormancy release. *Plant, Cell and Environment*, 43, 40-54.
906 <https://doi.org/10.1111/pce.13650>
- 907 Ma, Q., Huang, J., Hänninen, H., Li, X., & Berninger, F. (2020). Climate warming prolongs the
908 time interval between leaf-out and flowering in temperate trees: effects of chilling, forcing
909 and photoperiod. *Journal of Ecology*. <https://doi.org/10.1111/1365-2745.13558>.
- 910 Marino, G.P., Kaiser, D.P., Gu, L., Ricciuto, D.M. (2011) Reconstruction of false spring
911 occurrences over the southeastern United States, 1901-2007: an increasing risk of spring
912 freeze damage? *Environmental Research Letters*, 6, 024015.
- 913 Martínez-Lüscher, J., Hadley, P., Ordidge, M., Xu, X., & Luedeling, E. (2017). Delayed chilling
914 appears to counteract lowering advances of apricot in southern UK. *Agricultural and Forest
915 Meteorology*, 237-238, 209-218.
- 916 Meinshausen, M., Smith, S., Calvin, K.V., Daniel, J., Kainuma, M., Lamarque, J. F., ... Vuuren, D.
917 (2011). The RCP greenhouse gas concentrations and their extensions from 1765 to 2300.
918 *Climatic Change*, 109, 213-241. <https://doi.org/10.1007/s10584-011-0156-z>
- 919 Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., & Züst, A. (2006).
920 European phenological response to climate change matches the warming pattern. *Global
921 Change Biology*, 12, 1969-1976.

- 922 Murray, M.B., Cannell, M.G.R., & Smith, R.I. (1989). Date of budburst of fifteen tree species in
923 Britain following climatic warming. *Journal of Applied Ecology*, 26, 693-700.
- 924 Murray, M.B., Smith, R.I., Leith, I.D., Fowler, D., Lee, H.S.J., Friend, A.D., & Jarvis, P.G. (1994).
925 Effects of elevated CO₂, nutrition and climatic warming on bud phenology in Sitka spruce
926 (*Picea sitchensis*) and their impact on the risk of frost damage. *Tree Physiology*, 14, 691-
927 706.
- 928 Nizinski, J.J., & Saugier, B. (1988). A model of leaf budding and development for a mature *Quercus*
929 forest. *Journal of Applied Ecology*, 25, 643-652.
- 930 Perry, T.O. (1971). Dormancy of trees in winter. *Science*, 171, 29-36.
- 931 Polgar, C.A., & Primack, R.B. (2011). Leaf-out phenology of temperate woody plants: from trees to
932 ecosystems. *New Phytologist*, 191, 926-941.
- 933 R Development Core Team. (2020). *R: A language and environment for statistical computing*.
934 Vienna, Austria: R Foundation for Statistical Computing. Retrieved from [https://www.R-](https://www.R-project.org/)
935 [project.org/](https://www.R-project.org/)
- 936 Réaumur, M de. 1735. *Observations du thermomètre faites à Paris pendant l'année 1735 comparées*
937 *avec celles qui ont été faites sous la ligne à l' Ile de France, à Alger et en quelques-unes de*
938 *nos îles de l'Amérique*. Académie royale des sciences – Année 1735.
- 939 Ren, S., Long, C., Zhou, X., Zhang, C., & Zhou, Q. (2017). *Torreya grandis* cultivation
940 management technology of Guizhou botanical garden in different phenological period.
941 *Guizhou Science*, 35(4), 29-32. <https://doi.org/10.3969/j.issn.1003-6563.2017.04.007> (in
942 Chinese)
- 943 Richardson, A.D., Hollinger, D.Y., Dail, D.B., Lee, J.T., Munger, J.W., & O'Keefe, J. (2009)
944 Influence of spring phenology on seasonal and annual carbon balance in two contrasting
945 New England forests. *Tree Physiology*, 29, 321-331.
- 946 Richardson, E.A., Seeley, S.D., & Walker, D.R. (1974). A model for estimating the completion of

- rest for 'Redhaven' and 'Elberta' peach trees. *HortScience*, 9, 331-332.
- Rohde, A., & Bhalerao, R.P. (2007). Plant dormancy in the perennial context. *Trends in Plant Science*, 12, 217-223.
- Sarvas, R. (1972). Investigations on the annual cycle of development of forest trees. Active period. *Communicationes Instituti Forestalis Fenniae*, 76(3), 1-110.
- Sarvas, R. (1974). Investigations on the annual cycle of development of forest trees. II. Autumn dormancy and winter dormancy. *Communicationes Instituti Forestalis Fenniae*, 84(1), 1-101.
- Senior, V.L., Evans, L.C., Leather, S.R., Oliver, T.H., & Evans, K.L. 2020. Phenological responses in a sycamore-aphid-parasitoid system and consequences for aphid population dynamics: A 20 year case study. *Global Change Biology*, 26, 2814-2828.
- <https://doi.org/10.1111/gcb.15015>
- Song, Z., Song, X., Pan, Y., Dai, K., Shou, J., Chen, Q., ... & Du, Y. (2020). Effects of winter chilling and photoperiod on leaf-out and flowering in a subtropical evergreen broadleaved forest in China. *Forest Ecology and Management*, 458, 117766.
- Sutinen, S., Partanen, J., Viherä-Aarnio, A., & Häkkinen, R. (2012). Development and growth of primordial shoots in Norway spruce buds before visible bud burst in relation to time and temperature in the field. *Tree Physiology*, 32, 987-997.
- Taylor, K., Ronald, S., & Meehl, G. (2011). An overview of CMIP5 and the Experiment Design. *Bulletin of the American Meteorological Society*, 93, 485-498.
- <https://doi.org/10.1175/BAMS-D-11-00094.1>
- Thrasher, B., Maurer, E. P., McKellar, C., & Duffy, P. B. (2012). Technical Note: Bias correcting climate model simulated daily temperature extremes with quantile mapping. *Hydrology and Earth System Sciences*, 16(9), 3309-3314. <https://doi.org/10.5194/hessd-9-5515-2012>
- Tylewicz, S., Petterle, A., Marttila, S., Miskolczi, P., Azeez, A., Singh, R.K., ... & Bhalerao, R.P.

- 972 (2018). Photoperiodic control of seasonal growth is mediated by ABA acting on cell-cell
973 communication. *Science*, 360, 212-215.
- 974 Vegis, A. (1964). Dormancy in higher plants. *Annual Review of Plant Physiology*, 15, 185-224.
- 975 Viherä-Aarnio, A., Sutinen, S., Partanen, J., & Häkkinen, R. (2014). Internal development of
976 vegetative buds of Norway spruce trees in relation to accumulated chilling and forcing
977 temperatures. *Tree Physiology*, 34, 547-556.
- 978 Vitasse, Y. (2013). Ontogenic changes rather than difference in temperature cause understory trees
979 to leaf out earlier. *New Phytologist*, 198, 149-155.
- 980 Vitasse, Y., & Basler, D. (2013). What role for photoperiod in the bud burst phenology of European
981 beech. *European Journal of Forest Research*, 132, 1-8.
- 982 Wang, J.Y. (1960). A critique of the heat unit approach to plant response studies. *Ecology*, 41, 785-
983 790.
- 984 Wang, H., Wu, C., Ciais, P., Peñuelas, J., Dai, J., Fu, Y., & Ge, Q. (2020). Overestimation of the
985 effect of climatic warming on spring phenology due to misrepresentation of chilling. *Nature*
986 *Communications*, 11, 4945.
- 987 Weinberger, J.H. (1950). Chilling requirements in peach varieties. *Proceedings of the American*
988 *Society for Horticultural Science*, 56, 122-128.
- 989 Xu, Y., Dai, J., Ge, Q., Wang, H., & Tao, Z. (2020). Comparison of chilling and heat requirements
990 for leaf unfolding in deciduous woody species in temperate and subtropical China.
991 *International Journal of Biometeorology*. doi: 10.1007/s00484-020-02007-7.
- 992 Zettlemoyer, M.A., Schultheis, E.H., & Lau, J.A. (2019). Phenology in a warming world:
993 differences between native and non-native plant species. *Ecology Letters*, 22, 1253-1263.
- 994 Zhang, R., Lin, J., Wang, F., Shen, S., Wang, X., Rao, Y., ... & Hänninen H, 2021. The chilling
995 requirement of subtropical trees is fulfilled by high temperatures: A generalized hypothesis
996 for tree endodormancy release and a method for testing it. *Agricultural and Forest*

- 997 *Meteorology* (accepted).
- 998 Zhang, R., Wang, F., Zheng, J., Lin, J., Hänninen, H., & Wu, J. (2020). Chilling accumulation and
 999 photoperiod regulate rest break and bud burst in five subtropical tree species. *Forest*
 1000 *Ecology and Management*. doi:10.1016/j.foreco.2020.118813.
- 1001 Zheng, Z., Zhu, W., Chen, G., Jiang, N., Fan, D., & Zhang, D. (2016) Continuous but diverse
 1002 advancement of spring-summer phenology in response to climate warming across the
 1003 Qinghai-Tibetan Plateau. *Agricultural and Forest Meteorology*, 223, 194-202.
- 1004 Zohner, C.M., Mo, L., Sebald, V., & Renner, S.S. (2020). Leaf-out in northern ecotypes of wide-
 1005 ranging trees requires less spring warming, enhancing the risk of spring frost damage at cold
 1006 limits. *Global Ecology and Biogeography*, 29, 1065-1072. doi.org/10.1111/geb.13088

1007 TABLES

1008 Table 1. Experimental temperatures applied in the Spring experiments of 2018 – 2020 for
 1009 formulating Sub-model II for each of the five material categories addressed in the study (seedlings
 1010 of three species and both seedlings and twigs representing adult trees of *Torreya*).

1011

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

1012

1013 Table 2. Duration of chilling, Δt , required at the experimental chilling temperatures for rest
1014 completion in the five material categories studied (seedlings of three species and both seedlings and
1015 twigs representing adult trees of *Torreya*). The values of Δt are indicated both in hours, as used in
1016 the modelling (Eqns. (1), (9); Table 4), and in days, as used in the plots to determine the values
1017 (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	-	-

1018

1019

1020

1021 Table 3. The stations where phenological records were collected and the corresponding meteorological stations that provided air temperature
 1022 data; both data sets were used in the present study for independent testing of process-based tree phenology models. For *Torreya*, the phenological
 1023 data comprised female flowering (Station 4, Ren et al., 2019); for all other species, the phenological data comprised the leafout of vegetative
 1024 buds in adult trees (Stations 1-3, Chinese National Ecology Science Data Center, www.cnern.org.cn). All temperature data were provided by the
 1025 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>

1026

1027 Table 4. Equations of Sub-model I for the five material categories studied (seedlings of three
1028 species and both seedlings and twigs representing adult trees of *Torreya*). Sub-model I represents
1029 the air temperature response of the rate of rest break, R_r (function f_1 in Eqn. 1 of the overall model;
1030 see Figure 2). In the modified model for each material category, the equations for all temperatures T
1031 $< +5$ °C are replaced by a constant value of R_r (dashed lines in Figure 2), either by using the
1032 constant value indicated by the shading (*Castanopsis* and *Phoebe* seedlings) or by calculating the
1033 constant value with the shaded equation with $T = +5$ °C (*Pseudolarix* and *Torreya* seedlings and
1034 *Torreya* trees).

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

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

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

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

1045 Table 6. Parameter values of Sub-model III (Eqn. 18) for the five material categories studied
 1046 (seedlings of three species and both seedlings and twigs representing adult trees of *Torreya*). Sub-
 1047 model III mediates the effect of the rest status on the rate of ontogenetic development towards bud
 1048 burst (Figure 1) by formulating the dependence of ontogenetic development, C_o , on the state of rest
 1049 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

1050

1051

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

FIGURE LEGENDS

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

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

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

1088 in one hour. The value $R_{o,pot} = 0.2 \text{ \% hour}^{-1}$, for instance, implies that at the particular temperature,
1089 500 hours after rest completion are required for leafout/flowering

1090 **FIGURE 4** Sub-model IIII for each of the five material categories examined, representing the
1091 dependency of ontogenetic competence, C_o , on the state of rest break, S_r , (in the overall model,
1092 function f_3 in Eqn. 5). The data points were determined on the basis of the experimental results of
1093 Zhang et al. (2021). Function f_3 is formulated according to Eqn. (18) with the parameter values
1094 presented in Table 6. The value of S_r indicates the percentage of the physiological changes of rest
1095 break caused by chilling and required for rest completion that have taken place at a given moment.
1096 The value of C_o indicates the relative effect of the rest condition on the rate of ontogenetic
1097 development. With $C_o = 0.5$, for instance, twice as much time is required for leafout/flowering as is
1098 required after rest completion ($S_r = 100 \text{ \%}$) with $C_o = 1$

1099 **FIGURE 5** (a) Daily mean temperatures for the campus seedling collection (for seedlings of the
1100 four species in panels b-e) and for the *Torreya* tree plantation (for *Torreya* trees in panel f). (b-f)
1101 Predicted dormancy dynamics for autumn 2018 and spring 2019 of the five material categories
1102 addressed in the study. The vertical axis on the left represents the state of rest break, S_r , (blue line)
1103 and the state of ontogenetic development, S_o , (orange line). Rest completion is predicted to occur
1104 when $S_r = 100 \text{ \%}$ (date marked in a blue font) and leafout/flowering when $S_o = 100 \text{ \%}$ (date marked
1105 in an orange font). The observed leafout/flowering is marked with a circle and the date in a black
1106 font. The vertical axis on the right represents ontogenetic competence, C_o , (red line). By definition,
1107 $C_o = 1$ at rest completion, when $S_r = 100 \text{ \%}$. Otherwise the relationship between C_o and S_r varies
1108 among the five material categories as shown in Figure 4

1109 **FIGURE 6** Independent tests of the process-based spring phenology models developed for the four
1110 subtropical tree species by using both phenological records and results from our warming whole-
1111 tree chamber (WTC) experiment. The phenological records represent adult trees (flowering in

1112 *Torreya*, leafout in the other three species), whereas the results from the WTC experiment represent
 1113 leafout in the seedlings of all four species. The predictions for the phenological records of
 1114 *Castanopsis*, *Phoebe*, and *Pseudolarix* trees were calculated by means of the models developed for
 1115 seedlings because no model for adult trees had been developed for these species in the present study

1116 **FIGURE 7** Projected timing of spring phenology (flowering for *Torreya* trees, leafout for the
 1117 seedlings of the four species) for 2020 – 2100 under the climatic scenarios RCP4.5 and RCP8.5.
 1118 The projections were calculated by means of the process-based models developed in the present
 1119 study. The trends are presented here with direct lines fitted to the results; for the original yearly
 1120 results, see Figure S4

1121

FIGURE 1

FIGURE 2

FIGURE 3

FIGURE 4

FIGURE 5

FIGURE 6

FIGURE 7