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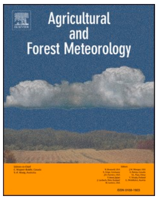

Discovering ecophysiological causes of different spring phenology responses of trees to climatic warming

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ABSTRACT

Global warming has generally advanced the spring phenology of extratropical trees. In several cases, however, the advancing has levelled off, indicating a declining temperature sensitivity of phenological timing. The potential reasons for the decline have been actively debated, but no direct experimental evidence has been produced to support any of the theories put forward. With the aid of scenario simulations, we examined which ecophysiological tree traits restrict the advancing of the onset of spring phenology in four subtropical tree species under global warming. In the simulations, we applied process-based tree spring phenology models formulated on the basis of results of experiments specifically designed for examining the ecophysiological responses addressed. We identified three restricting ecophysiological traits: 1) the chilling effect operates at relatively low temperatures only, 2) the temperature sensitivity of spring phenology is low in the temperature range of +10 to +20 °C which is critical under climatic warming in subtropical conditions; and 3) the winter rest is deep. Unexpectedly, a high chilling requirement was not included amongst the restricting ecophysiological traits. Our experimentally-based results show that the spring phenology of the trees under climatic warming is significantly affected by seemingly small and usually neglected details of the ecophysiological responses to chilling and forcing temperatures.

1. Introduction

In extratropical trees, the timing of spring leaf-out is a key ecological phenomenon. It affects several important ecological processes, such as the cycling of carbon, water, and nutrients; and ecosystem productivity (Kramer and Hänninen, 2009; Richardson et al., 2009; Keenan et al., 2014; Zhou et al., 2020). Similarly, the timing of flowering is essential for seed production in the trees (Danusevičius, 1987; Rousi et al., 2011). Spring phenology, including both the vegetative and the generative development, is ultimately an essential determinant of the geographical ranges of the tree species (Chuine and Beaubien, 2001; Chuine, 2010).

Analyses of long-term phenological and air temperature records have shown that global warming has advanced the spring phenology of temperate trees during the past few decades (Menzel and Fabian, 1999; Menzel et al., 2006; Linkosalo et al., 2009). However, some of these studies have also found a recent decline in this advancing, leading to an apparent decline in the temperature sensitivity (days per °C warming) of the spring phenology. This phenomenon has generally been attributed to winter warming and the subsequently decreased amount of chilling, which delays the completion of winter rest break, or to the restricting effects of photoperiod (Fu et al., 2015a; Piao et al., 2017; Chen et al., 2018; H. Zhang et al., 2022). However, Wolkovich et al. (2021) recently provided an alternative explanation, suggesting that the apparent decline of the temperature sensitivity may reflect a failure to address the

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non-linear temperature response of the spring development of the trees in the calculations.

The debate on the reason for the apparent decline of the temperature sensitivity of spring phenology shows the crucial importance of determining the true species-specific ecophysiological responses that regulate the spring phenology of trees. However, due to the high demands of labour and experimental facilities involved, these responses are not often determined experimentally (see, however Sarvas, 1972, 1974; Campbell and Sugano, 1975; Myking, 1997; Caffarra and Donnelly, 2011; Caffarra et al., 2011; Baumgarten et al., 2021; Zhang et al., 2022). Instead, models are usually built upon hypotheses that have been experimentally validated several decades earlier, with only a few species, or by estimating the parameters of the models solely on the basis of phenological records obtained by means of inverse modelling techniques, where the model parameters are estimated by fitting the model into observational phenological and air temperature records (Fu et al., 2015a, b; Basler, 2016; Chen et al., 2017; Ma et al., 2018, 2021; Chen et al., 2018, 2019; Du et al., 2019; Fu et al., 2019; Zohner et al., 2020; Wang et al., 2020; Luedeling et al., 2021). In the absence of direct experimentally determined ecophysiological responses, these indirect and approximate approaches have been necessary although they have been shown to be prone to various shortcomings and errors (Hunter and Lechowicz, 1992; Chuine et al., 2016; Hänninen et al., 2019; Wang et al., 2020).

Here, we took an ecophysiological approach to the process-based tree phenology modelling, with the aim to identify the ecophysiological causes of different spring phenology responses of trees to climatic warming in the subtropical conditions. Our study builds on our two previous studies (Fig. S1): R. Zhang et al. (2021) published most of the primary experimental data used in the modelling. Zhang et al. (2022) introduced the procedure for using the experimental results in the modelling, and they also formulated four of the models applied in the present study (i.e., four models for leaf-out in the respective four subtropical tree species, Fig. S1). In this study, using partly unpublished data we first formulate a fifth model (i.e., a model for flowering in one of the subtropical tree species, Fig. S1). Subsequently, as the main part of the study we use the five models, together with 12 modifications of them, in a modelling comparison to identify three physiological dormancy traits of the trees that slow down the advancing of spring phenology under global warming in subtropical conditions (Fig. S1). Our modelling comparison is a theoretical one: rather than differences between the examined species, or between flower buds and leaf buds, our focus is on the responses as such included in the models: which of them are critical to the response of the tree spring phenology to warming. Our results highlight the importance of explicitly addressing the ecophysiological phenomena that underlie the effects of chilling and forcing accumulation when the effects of climatic warming on the spring phenology of trees are projected.

2. Materials and methods

2.1. The HK framework for process-based tree spring phenology modelling

In the bi-phase process-based tree spring phenology models, two ecophysiological processes are addressed (Chuine et al., 2013): first, winter chilling is required for rest break (endodormancy release), which means removal of the physiological conditions in the bud that arrest (or delay) the occurrence of the spring phenological event (for the sake of brevity, the generic concept of 'bud burst' is used in the following for all spring phenological events addressed in the modelling). Second, spring forcing is required for ontogenetic development (ecodormancy release), i.e., the invisible anatomical development in the bud that leads to the visible bud burst. The models used in the present study were developed using the Hänninen-Kramer modelling framework (HK framework; Hänninen, 1990, 2016; Kramer, 1994a, b; Hänninen and Kramer, 2007). The framework is modular, as the models formulated within the framework consist of three sub-models, each one addressing the respective dormancy trait (Fig. 1). In addition to the rest break caused by winter chilling (Sub-model I) and the ontogenetic development caused by spring forcing (Sub-model II), a third model is used for transferring the growth arresting effects of rest condition to the ontogenetic development (ontogenetic competence, Sub-model III). In other words, Sub-model III transfers the effects of winter chilling to spring forcing. The equations of the modelling algorithm of the HK framework have been documented before (Hänninen, 1990, 2016; Kramer, 1994a, b; Hänninen and Kramer, 2007; Zhang et al., 2022), here a descriptive overview of the rationale of the framework is provided (Fig. 1).

After the chilling requirement is met the ambient air temperature solely regulates the rate of ontogenetic development towards bud burst. This is *the air temperature response of potential rate of ontogenetic development,* $R_{o,pot}$ (Sub-model II, black sigmoidal curve in the inlet on the left-hand side of Fig. 1). This response can take different forms with different tree species and bud types, that is why a separate sub-model is needed for this response (Fig. 2b).

Before the chilling requirement is met, the rate of ontogenetic development is lower than the potential one (blue and yellow sigmoidal curves in the inlet of Fig. 1), or it may be even zero (red horizontal line in the inlet). This effect of the rest condition on the rate of (the realized) ontogenetic development is modelled at two steps with the two respective sub-models. First, Sub-model I is used to address *the temperature response of rate of rest break,* $R_r(t)$. Here again a separate sub-model is needed, because this response can take different forms with different tree species and bud types (Fig. 2a). State of rest break, $S_r(t)$, is calculated by integrating $R_r(t)$ with respect to time (i.e., the hourly values of $R_r(t)$ are summed). $R_r(t)$ is defined on a percentage basis, so the chilling requirement of rest completion is predicted to be met when $S_r(t) = 100\%$.

The value of $S_r(t)$ indicates for any time instant t the percentage of the chilling accumulated at time instant t, out of the chilling requirement. However, there is also variation between species and bud types in the effect of the chilling accumulation on (the realized) rate of ontogenetic development. In order to address this variation, a theoretical variable called ontogenetic competence, C_o, is introduced in Sub-model III: *the dependence of ontogenetic competence,* C_o*, on the state of rest break,* S_r. Like in the two other traits addressed by Sub-models I and II, there is variation between tree species and bud type also in the trait addressed by Sub-model III (Fig. 2c). C_o is a [0,1] multiplier so that (the realized) rate of ontogenetic development, $R_o(t)$ is obtained by multiplying the potential rate, $R_{o,pot}$, by C_o (equation on top of Fig. 1). When $C_o = 0$, no ontogenetic development takes place ($R_o(t) = 0\ \%\ h^{-1}$, red line in the insert of Fig. 1). When $C_o = 1$, the value of $R_o(t)$ is equal to its potential value R_o (black sigmoidal curve in the insert of Fig. 1). Regardless of the other properties of the Sub-model III, by definition C_o attains the value of unity when rest is completed and the phase of quiescence is attained at $S_r(t) = 100\%$ (Fig. 2). When $0 < C_o < 1$, the rate of ontogenetic development is lower than the potential rate (blue and yellow sigmoidal curves in the insert of Fig. 1). State of ontogenetic development, $S_o(t)$, is calculated by integrating $R_o(t)$ with respect to time (i.e., the hourly values of $R_o(t)$ are summed). Similarly to $R_r(t)$, $R_o(t)$ is defined on a percentage basis, so the bud burst is predicted to occur when $S_o(t) = 100\%$.

Introduction of the Sub-model III makes the framework flexible so that ecophysiologically different tree properties can be addressed with the same modelling rationale and algorithm. The bi-phase process-based tree phenology models have been classically sub-divided into the sequential and the parallel models (Fig. S2a; Chuine et al., 2013; Hänninen, 2016). In the sequential model chilling is accumulated (rest break is simulated) first, and only after meeting the chilling requirement forcing is accumulated (ontogenetic development is simulated). Ecophysiologically, an abrupt rest break, with a clear border between the rest and quiescence periods, is assumed. In the parallel model, on the contrary, both chilling and forcing are accumulated simultaneously, but

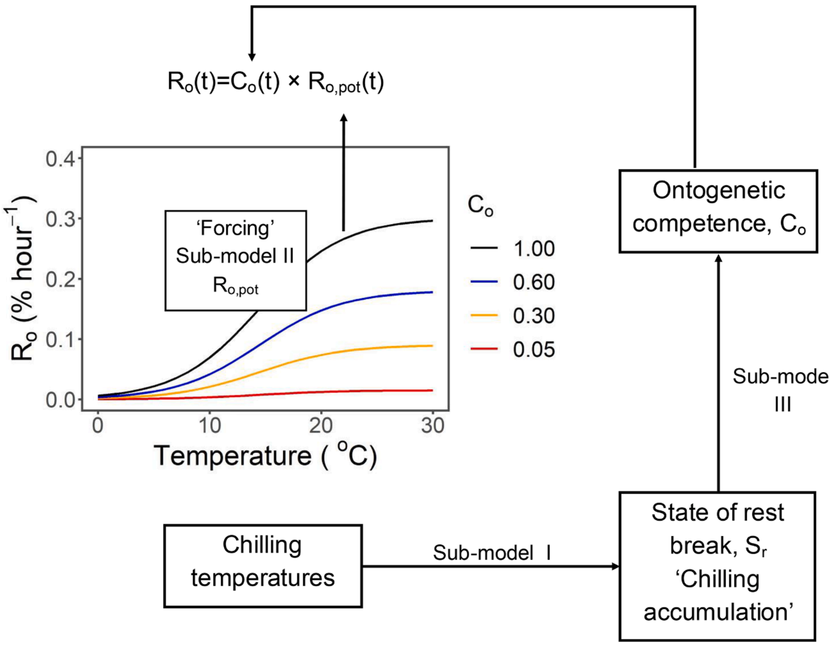

Fig. 1. The modular Hänninen-Kramer (HK) modelling framework used in the present study to examine the ecophysiological dormancy traits regulating the spring phenology in four subtropical tree species. For details, see the section *The HK framework for process-based tree spring phenology modelling.*

the rate of forcing accumulation increases with increasing previous accumulation of chilling. As elaborated by the flexible Sub-model III, the dependence can take also any intermittent form between these two extremes (Fig. S2b). In this way, a continuum of responses from the sequential end to the parallel end can be addressed within the same modelling framework.

Sub-model III provides also a measure of the depth of rest. When the dependence of C_o on S_r is steep, then chilling has a big influence on the occurrence and timing of bud burst (deep rest, Fig. S3), but when the dependence is gently sloping, the effect of chilling on bud burst timing is small (shallow rest, Fig. S3). Notice that the depth of rest is a different trait, as compared with the chilling requirement. The chilling requirement defines, how long chilling is needed at each temperature for S_r to increase from 0 to 100% (Δt in Fig. S4). The chilling requirement, Δt, is not seen directly in any of the three sub-models. However, because rate of rest break, R_r, is determined as being inversely proportional to Δt ($R_r = 100/\Delta t$, Zhang et al. 2022), the chilling requirement is represented by the level of the temperature response in Fig. (2a): the higher the chilling requirement, the lower the rate of rest break, R_r. So, both deep and shallow rest can be combined both with a high and a low chilling requirement.

The functioning of the overall model, and particularly the role of the Sub-model III in it, is best understood by comparing the time courses of the related variables illustrated between different species and bud types. See Fig. S5 in the *Results and Discussion* section.

2.2. Three categories of process-based tree phenology models used

The modelling comparison of the present study was carried out with three different categories of the process-based models (Fig. S1). First, we used the four models developed by Zhang et al. (2022) for seedling leaf-out in four subtropical tree species commonly used for afforestation in our study area: *Castanopsis sclerophylla* (Chinese Tanbark-oak), *Phoebe chekiangensis* (Zhejiang Phoebe), *Pseudolarix amabilis* (Golden larch), and *Torreya grandis* (Chinese Torreya).

Second, we used a new model developed in the present study for flowering in adult *Torreya grandis. Torreya* is an evergreen species, in which flower buds and leaf buds develop independently, and both of them overwinter. *Torreya* flowers from late March to early April, and leaf-out takes place after flowering. The model for *Torreya* flowering was developed using the same procedure Zhang et al. (2022) used for developing the seedling leaf-out models for the four species (see preceding paragraph). For developing the new *Torreya* flowering model, both previously published (Sub-models I and III, R. Zhang et al., 2021) and previously unpublished (Sub-model II) data were used (Fig. S1).

Third, we used models for 12 Theoretical Tree Genotypes, TTGs. The models for the TTGs were developed by various new combinations of the original sub-models of the five models developed for leaf-out in real seedlings, or flowering in real adult trees (see Section *Sensitivity analysis with TTGs* below).

2.3. Process-based model for Torreya flowering developed in the present study

Each sub-model was developed on the basis of an experiment especially designed for examining the particular dormancy trait addressed by the sub-model (Zhang et al., 2022). In brief, the data for Sub-model I (air temperature response of the rate of rest break) were gathered by exposing the experimental twigs to variable durations of controlled chilling at four constant chilling temperatures in the autumn. The twigs were then transferred to a regrowth test with constant forcing temperature conditions, and the occurrence and timing of flowering was recorded. These primary data obtained from R. Zhang et al. (2021) were used in the present study for inferring the chilling requirement Δt, i.e., the time required for rest completion in each chilling condition (Fig. S4). The empirical value of the rate of rest break for each constant chilling temperature was determined as 100/Δt. Finally, piece-wise linear curves were fitted to the data to represent the air temperature response of the rate of rest break (Fig. 2a, see also Fig. 3a in the *Results and Discussion* section).

The data for Sub-model II were collected in the present study by exposing fully chilled twigs to various constant air temperatures ranging from +10 to +28 °C in the spring and recording the date of flowering. The experimental conditions were the same as used earlier by Zhang et al. (2022) for developing the Sub-models II for the seedlings of the four species (Fig. S1). The potential rate of ontogenetic development was determined for each constant forcing temperature as 100/DBB, where DBB is the number of days required for flowering in the forcing

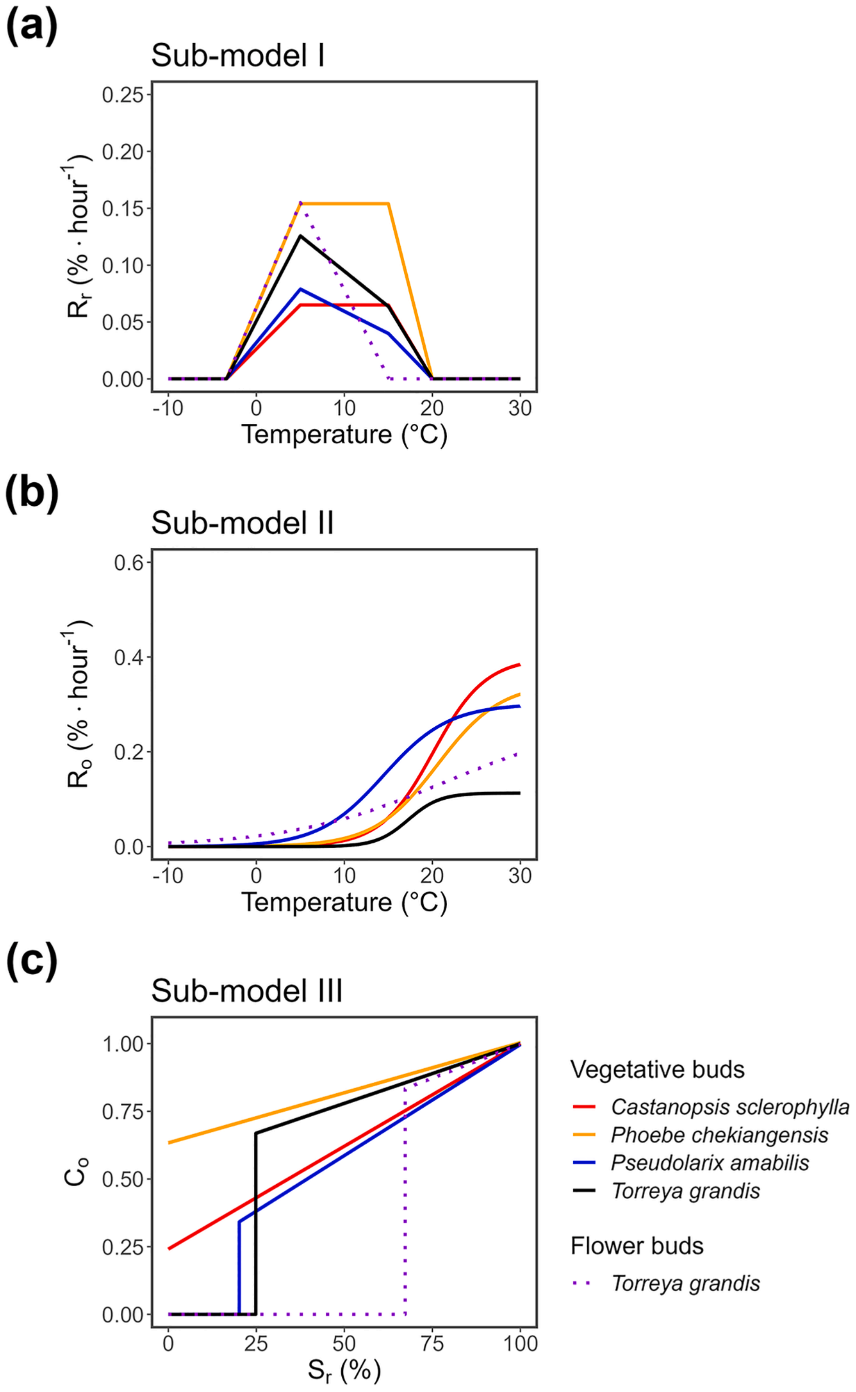

Fig. 2. Experimentally based air temperature responses of the dormancy processes that regulate the spring phenology in four subtropical tree species. The responses for leaf-out in the vegetative buds of *Castanopsis sclerophylla, Phoebe chekiangensis, Pseudolarix amabilis*, and *Torreya grandis* (solid lines) were adopted from Zhang et al. (2022). The responses for the flower buds of *Torreya grandis* trees were determined experimentally in the present study (dashed lines, Fig. 3 in the section *Results and Discussion*). (a) Air temperature response of the rate of rest break ('chilling', Sub-model I). (b) Air temperature response of the potential rate of ontogenetic development, $R_{o,pot}$ ('forcing', Sub-model II). (c) Ontogenetic competence, C_o, as a function of the state of rest break, S_r (Sub-model III).

conditions. Lastly, a sigmoidal curve was fitted to the data (Fig. 2b; see also Fig. 3b in the *Results and Discussion* section).

The primary data for Sub-model III were collected from the same chilling-forcing experiment as was used for formulating Sub-model I (R. Zhang et al., 2021). In the present study, the empirical value of ontogenetic competence was determined for each duration of chilling x as the ratio of DBB obtained at rest completion (Fig. S4) to its value obtained after x days of chilling. Finally, piece-wise linear curves were fitted to the data (Fig. 2c; see also Fig. 3c in the *Results and Discussion* section). For other details of the experimental methods and model formulation, see R. Zhang et al. (2021, R. 2022) (Fig. S1).

The model developed for *Torreya* flowering was tested against independent flowering observations for 2014–2016 from Guiyang (26°34′ N, 106°42′ E) and climatic records from a nearby meteorological station (26°21′ N, 106°26′ E).

2.4. *Model projections to future climate conditions*

The four process-based models developed earlier for leaf-out in the seedlings of the four species (Zhang et al. 2022) and the model developed in the present study for the flowering in adult *Torreya grandis* trees (Fig. 2) were used for assessing the effects of global warming on the timing of leaf-out and flowering in Hangzhou, south-eastern China (30°08′N, 120°06′E) in 2020 – 2099. The simulations were based on daily minimum and maximum temperatures from the scenarios RCP4.5 and RCP8.5, representing warming by 1.4 and 4.8 °C, respectively, for the period of 2020 – 2100 in Hangzhou (Meinshausen et al., 2011; Thrasher et al., 2012). Our models work with an hourly time step, so that

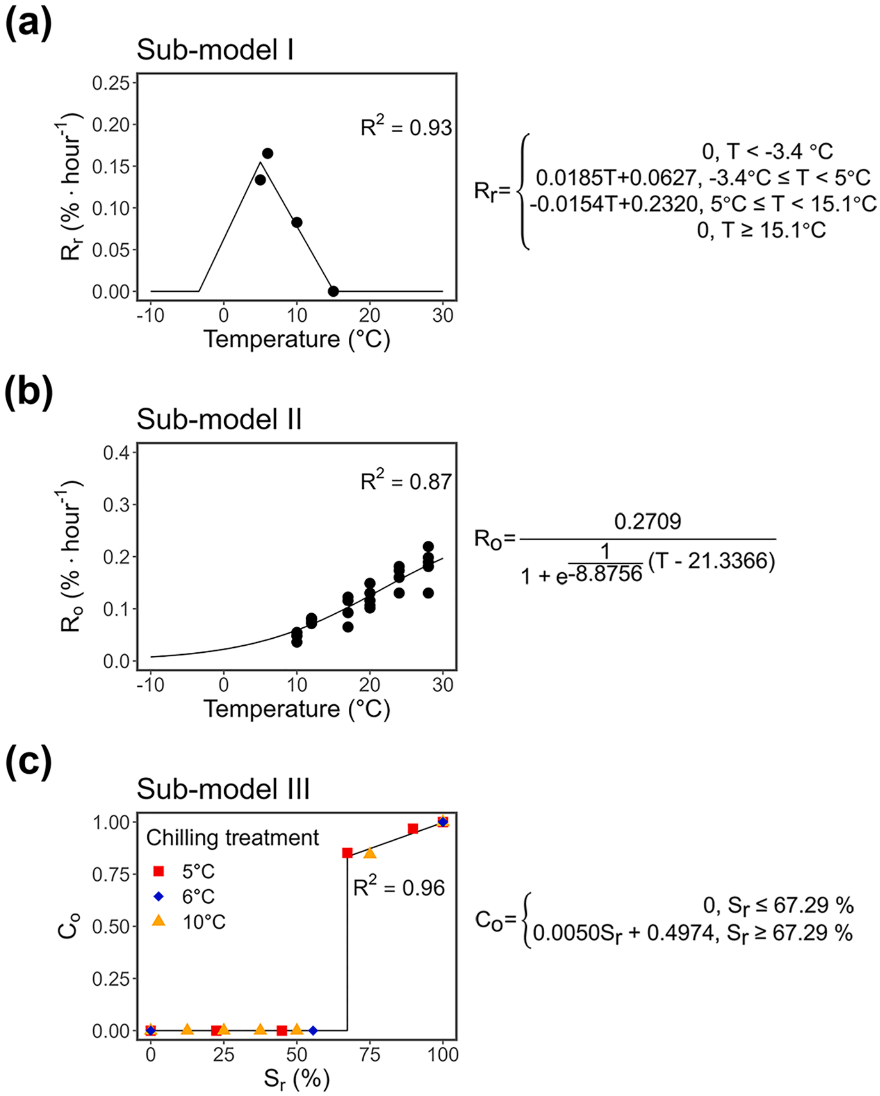

Fig. 3. A process-based tree phenology model developed in the present study for the spring phenology of the flowering of subtropical *Torreya grandis* trees. (a) Air temperature response of the rate of rest break (‘chilling’, Sub-model I). (b) Air temperature response of the potential rate of ontogenetic development, $R_{o,pot}$ (‘forcing’, Sub-model II). (c) Ontogenetic competence, C_o, as a function of the state of rest break, S_r (Sub-model III). No rest break was seen at +15 °C ($R_r(15) = 0\%\ h^{-1}$, see panel (a), so that the results for Sub-model III were available for +5 °C, +6 °C, and +10 °C only. The fitted curves are identical to the dashed curves in the summary Fig. 2.

we converted the daily temperature data into hourly temperatures for the model projections, following Zohner et al. (2020). The simulations were started each year on 23 November (Zhang et al., 2022). The projected yearly times of leaf-out / flowering were plotted against the year and a linear regression was fitted to the data. The slope of the regression represented the advancing (or delaying) rate of spring phenology caused by warming.

2.5. *Sensitivity analysis with TTGs*

In the simulations with scenarios RCP4.5 and RCP8.5, we found an exceptionally low advancing of the flowering date of *Torreya*. The role of each of the three ecophysiological dormancy traits represented by the three respective sub-models (Fig. 2) in determining the spring phenology under climatic warming was examined in a sensitivity analysis where the projected spring phenology of *Torreya* flowering (see previous paragraph) was compared with the projected spring phenology of theoretical tree genotypes, TTGs. Similarly to the simulations for *Torreya* flowering, also the simulations with the TTGs were started each year on 23 November (Zhang et al., 2022). The TTGs were constructed by replacing in the model of *Torreya* flower buds one sub-model at a time with the corresponding sub-model obtained for the leaf-out in the seedlings of one of the four species. In this way 3 (number of sub-models in the *Torreya* flowering model) x 4 (number of the replacing options for each sub-model) =12 TTGs were constructed (Table S1). The sensitivity analysis was based on this principle: if the trait described by a given sub-model causes the low advancing rate found for *Torreya* flowering under climatic warming, then a TTG where that particular sub-model is replaced will project a higher advancing rate, as compared with the rate projected by the *Torreya* flowering model. The differences in the effects of the three ecophysiological dormancy traits represented by the three corresponding sub-models were tested statistically with a one-way ANOVA.

3. Results and discussion

3.1. *Model for Torreya flowering*

Going from +5 °C towards higher temperatures, the rate of rest break decreased, reaching zero at +15 °C (Sub-model I, Fig. 3a). For temperatures below +5 °C, there were no data available, so that on the basis of experimental results for a boreal *Betula* species (Sarvas, 1974), the rate of rest break was assumed to decline going from +5 °C towards lower temperatures, reaching zero at −3.4 °C (Zhang et al., 2022). In all, then, a bell-shaped temperature response curve was obtained for Sub-model I, representing the temperature response of the rate of rest break (Fig. 3a). For Sub-model II, representing the temperature response of the potential rate of ontogenetic development, a sigmoidal response curve was obtained (Fig. 3b).

For Sub-model III, representing the dependence of ontogenetic competence, C_o, on the state of rest break (accumulated chilling), a piece-wise linear response curve typical for the intermittent model (Fig. S2b) was obtained (Fig. 3c). According to the response, no ontogenetic development is possible ($C_o = 0$) until the accumulated chilling reaches 67% of the chilling requirement. With further chilling after that, nearly full ontogenetic competence is attained abruptly (Fig. 3c). This response indicates a deep winter rest, i.e., a great effect of the accumulated chilling on the ontogenetic development towards flowering (Fig. S3). This is seen especially when the Sub-model III for *Torreya* flowering is compared with corresponding sub-models developed earlier for leaf-out in *Castanopsis* and *Phoebe*, where chilling accumulation has a smaller effect on the ontogenetic competence, C_o (Fig. 2c). A full comparison of all three sub-models of *Torreya* flowering with corresponding sub-models developed earlier for the leaf-out in the four species examined (Fig. 2) will be presented below. In the test carried out with independent observational data, the flowering model predicted the observations of *Torreya* flowering in natural conditions with the RMSE at 4.6 days.

3.2. *Projected spring phenology*

The spring phenology was advanced in all scenario simulations projecting the effects of global warming on four subtropical tree species in 2020 – 2100 in Hangzhou, south-eastern China (Figs. 4,5). However, a major difference was found between the flowering of *Torreya grandis* trees and the leaf-out in the four examined species. Amongst them, the advancing rates of leaf-out varied between 0.4 and 0.8 days per decade for RCP4.5 and between 2.8 and 3.4 days per decade for RCP8.5 (Fig. 4). The projected advancing rates in leaf-out per one °C warming varied between 4.7 and 5.9 days / °C, with no major differences, in general, between the two climate scenarios (Fig. 5). These projected advancing rates per one °C warming are in line with the corresponding projections obtained in earlier studies with temperate tree species (Kramer, 1994b; Murray et al., 1994; Wang et al., 2020). For *Torreya* flowering, on the contrary, much lower advancing rates (0.4 and 0.6 days per decade for RCP4.5 and RCP8.5, respectively) were projected (Fig. 4); and there was a major difference between the advancing rate per °C warming projected for RCP4.5 (2.3 days per °C) and for RCP8.5 (0.9 days per °C) (Fig. 5).

On the basis of the earlier studies emphasizing the chilling requirement as a major factor counteracting the advancing effect of increased spring forcing on spring phenology (Murray et al., 1989; Hänninen, 1991; Fu et al., 2015a; Ford et al., 2016; Zhang et al., 2022), one would hypothesize that the counteracting effect is stronger in species and bud types with a high chilling requirement than in those with a low one. Accordingly, the relatively low advancing rate of *Torreya* flowering, as compared with the advancing rates of leaf-out in the four species (Fig. 4), might have been caused by a higher chilling requirement in the *Torreya* flower buds. That explanation implies that the rate of rest break, R_r, should be lower in *Torreya* flower buds than in the vegetative buds of the four species examined, because rest completion in *Torreya* flower buds would require a longer time in the chilling conditions (Fig. S4; for the reciprocal relationship between the chilling requirement and the rate of rest break, see section *Process-based model for* Torreya *flowering developed in the present study* above). However, the experimentally based air temperature responses of the rate of rest break showed no such difference (Fig. 2a). Actually, the value of R_r measured at +5 °C was the highest in the *Torreya* flower buds (together with the vegetative buds of *Phoebe chekiangensis*, Fig. 2a), indicating that the chilling requirement was the smallest in the *Torreya* flower buds. This finding shows that the reason for the deviating results for *Torreya* flowering is to be found elsewhere amongst the three ecophysiological dormancy traits addressed (Fig. 2). We identified three traits that explain the difference.

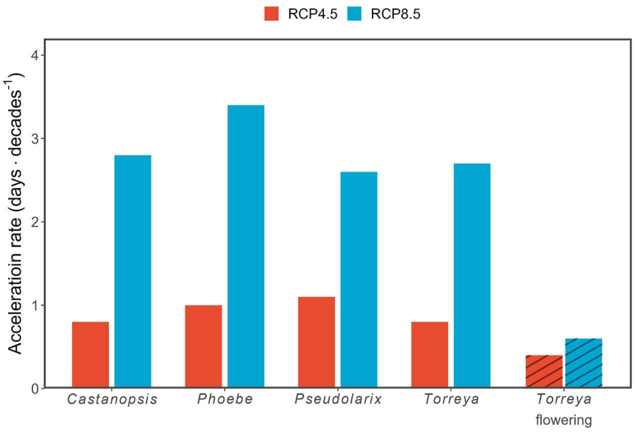

Fig. 4. Advancing rates of spring phenology in four subtropical tree species projected for 2020 – 2100 in Hangzhou, south-eastern China, under the warming scenarios RCP4.5 and RCP8.5. The rates are shown separately for leaf-out in the vegetative buds of each of the four tree species examined (bars without oblique lines) and flowering in flower buds of *Torreya grandis* trees (bars with oblique lines).

First, contrary to the vegetative buds of the four species, rest break in *Torreya* tree flower buds proceeds relatively slowly at temperatures above +12 °C, and not at all at temperatures above +15 °C (Figs. 2a, 3a). In the future, then, an increasing part of autumn and winter will be too warm to promote rest break in *Torreya* flower buds, thus delaying rest break, and consequently counteracting the advancing of flowering caused by warming in the spring (Table 1; the trait 'Low upper threshold of the rest-breaking chilling temperature range').

Second, in comparison with the vegetative buds of the four species, the rate of ontogenetic development in the flower buds in *Torreya* trees shows a smaller increase in the temperature range of +10 to +20 °C (Fig. 2b). These temperatures occur frequently in the subtropical winter and spring under climate warming, so sensitivity to these temperatures is critical in these conditions. Accordingly, this trait, 'Low temperature sensitivity of bud burst in the critical temperature range under warming' (Table 1), also provides a partial explanation for the minor advancing projected for *Torreya* flowering.

Third, the flower buds of *Torreya* trees do not respond to forcing temperatures by showing ontogenetic development at all before their rest break is almost completed as a result of chilling accumulation (S_r = 67%, Figs. 2c, S5). This is in striking contrast with the vegetative buds of *Castanopsis sclerophylla* and *Phoebe*, which respond to forcing temperatures, yet at a reduced rate, even without chilling (S_r = 0%, Figs. 2c, S5). The vegetative buds of *Pseudolarix amabilis* and *Torreya* show an intermediate position in this respect (Figs. 2c, S5). These differences address the depth of the rest, which is shallow in *Castanopsis* and *Phoebe* and deep in *Torreya* flower buds (Fig. 2c, compare with Fig. S3). Accordingly, the trait 'Deep rest' (Table 1) is the third one contributing to the minor advancing projected for *Torreya* flowering under warming.

We tested the conclusions gathered in Table 1 by a sensitivity analysis, which was made possible by our modular modelling framework that allows new combinations of the sub-models for different model comparisons (Hänninen, 2006) (Figs. 1, 2; Table S1). In the sensitivity analysis the results projected for *Torreya* flowering were compared with the corresponding results projected for 12 theoretical tree genotypes, TTGs (see section *Sensitivity analysis with TTGs* above). Under both climate scenarios, the advancing rate of the spring phenology was projected to be always higher in all TTGs than in *Torreya* flowering (Fig. 6). This confirms that all the three tree traits identified above (Table 1) on the basis of visual comparisons of the responses (Fig. 2) contribute to the minor advancing rate of *Torreya* flowering under climate warming (Fig. 4).

The sensitivity analysis further showed that amongst the three identified dormancy traits, the low temperature sensitivity of bud burst in the critical temperature range under warming (Table 1) had the

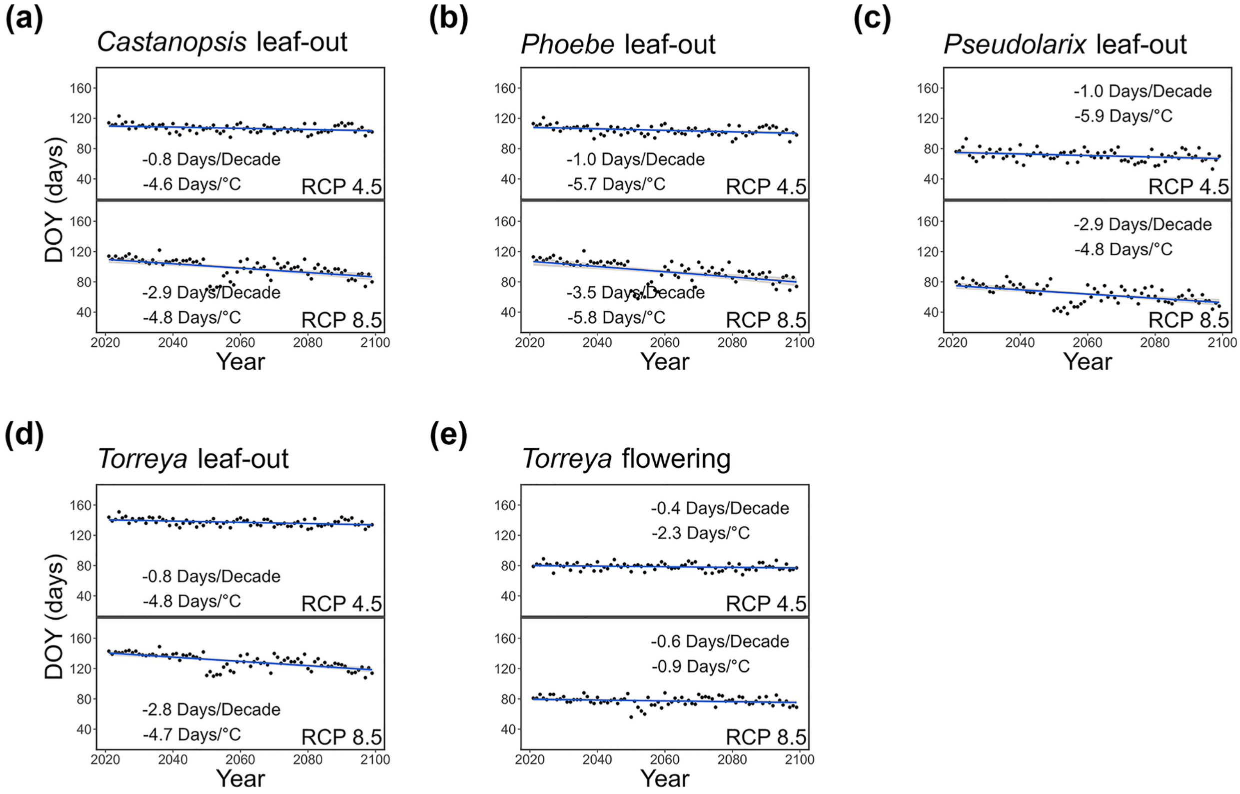

Fig. 5. Projected timing of the spring phenology in four subtropical tree species in Hangzhou, south-eastern China, for 2020 – 2100 under the climatic scenarios RCP4.5 and RCP8.5. Leaf-out in (a) *Castanopsis sclerophylla*, (b) *Phoebe chekiangensis*, (c) *Pseudolarix amabilis*, and (d) *Torreya grandis*; and (e) flowering in the flower buds of *Torreya grandis* trees.

Table 1
Three ecophysiological tree dormancy traits restricting the advancing of the flowering of *Torreya grandis* trees under climatic warming in subtropical conditions. Each of the three traits is seen in the corresponding panel of Fig. 2 as the difference between the temperature response of *Torreya* flower buds (dashed line) and the corresponding four other responses (solid lines) shown in the panel. The exact threshold temperatures indicated in the table are those found for the relatively warm subtropical conditions examined in the present study. .

Trait	Sub-model	Explanation
Low upper threshold of the rest-breaking chilling temperature range	I (Fig. 2a)	No rest break at temperatures above +15 °C. A large part of the future warm winters in subtropical conditions is too warm for rest break.
Low temperature sensitivity of bud burst in the critical temperature range under warming	II (Fig. 2b)	The increase in the rate of ontogenetic development towards bud burst is relatively small when the temperature rises from +10 to +20 °C. In subtropical conditions, that temperature range is critical in winter and spring under warming.
Deep rest	III (Fig. 2c)	The rest condition blocks all ontogenetic development towards bud burst until a large part (67%, Fig. 2c) of the chilling requirement has been accumulated. For comparison: the vegetative buds of *Castanopsis* and *Phoebe* have a shallow rest, with even non-chilled buds developing towards bud burst.

Note: for the sake of brevity, the concept ‘bud burst’ is used in a generic sense in the table, including all spring phenological phenomena of trees, such as the leaf-out of vegetative buds and the flowering of flower buds.

greatest restricting effect on the advancing of spring phenology (Fig. 6d). It is noteworthy that this mechanism has nothing to do with the chilling requirement, which is usually regarded as the main trait restricting the spring phenology advancing caused by increased forcing (Murray et al., 1989; Hänninen, 1991; Fu et al., 2015a; Ford et al., 2016; Zhang et al., 2022). The third trait we identified (Deep rest, Table 1) is also conceptually independent from the concept of chilling requirement. This is because deep rest can be associated with a low chilling requirement, and correspondingly, shallow rest can be associated with a high chilling requirement (Fig. S3). These two traits are, however, closely related to each other because the depth of rest determines how great an effect the chilling accumulation will have on the timing of spring phenology (Fig. 2c).

Our results are in line with those of Wolkovich et al. (2021) in that they emphasize the importance of non-linear temperature responses for regulating the spring phenology of trees. In accordance with the reasoning of Wolkovich et al. (2021), we projected no change in the temperature sensitivity of spring phenology, i.e., change in the advancing rate of spring phenology, when projecting the spring phenology under climatic warming with our non-linear models. This was true for both the real examined tree species (Fig. 5) and the theoretical tree genotypes, TTGs, used in the sensitivity analysis (Fig. 7).

3.3. Implications for climate change impact assessments

Our results have several specific implications for the process-based modelling of the spring phenology of trees and the application of these models to climatic change impact assessments.

First, in any consideration of the chilling requirement (Fig. S4) as a factor counteracting the advancing effect of warming on spring phenology, the variation between species in the location of the chilling curve on the temperature axis needs to be taken into account. In other words, the topical question of what temperatures are chilling

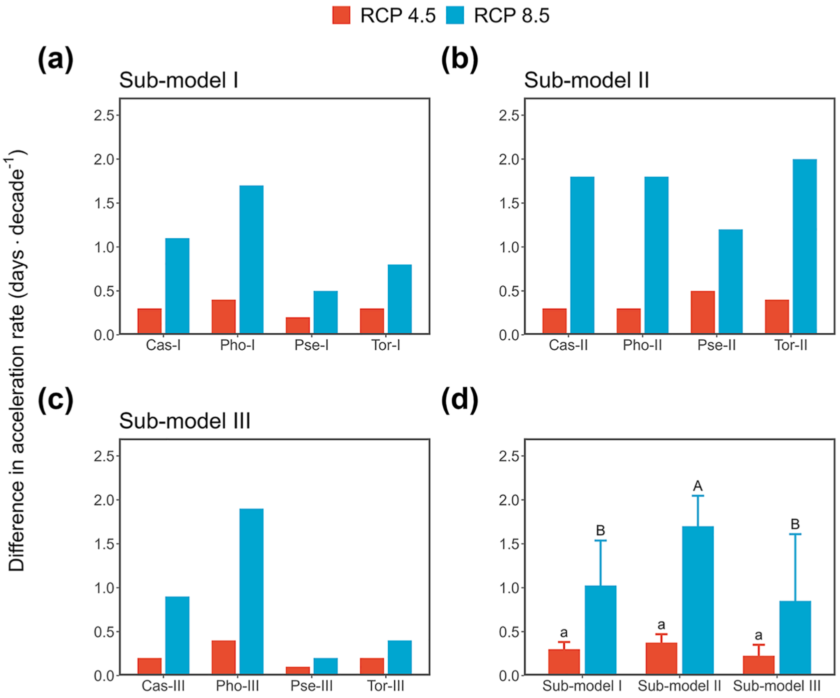

Fig. 6. A sensitivity analysis for discovering the ecophysiological dormancy traits responsible for the lower advancing rate of flowering projected for *Torreya grandis* in future climatic conditions (Fig. 4). Besides *Torreya* flowering, the timing of spring phenology under the warming scenarios RCP4.5 and RCP8.5 was also projected for twelve theoretical tree genotypes (TTGs). For the TTGs, the process-based tree phenology model of *Torreya* flowering was used (Fig. 3, dashed lines in Fig. 2), except that out of the three sub-models one sub-model at a time was replaced with the corresponding sub-model developed for leaf-out in the vegetative buds of one of the four tree species examined (solid lines in Fig. 2). The species is indicated by a three-letter abbreviation in the name of the TTG at the bottom of each bar, with the Roman numeral indicating the replaced sub-model (Table S1). The vertical axes indicate the difference in the advancing rate between the respective theoretical TTG and *Torreya* flowering, with positive values indicating a greater advancing rate for the TTG. (a) Simulations where Sub-model I was replaced. (b) Simulations where Sub-model II was replaced. (c) Simulations where Sub-model III was replaced. (d) For each of the three sub-models I – III (panels a-c), now shown on the horizontal axis, the mean ± SD of the differences reported in each of the panels a-c separately for each of the four species. Bars with different uppercase letters indicate significant differences ($p < 0.05$) between the three sub-models for RCP8.5. The corresponding differences for RCP4.5 were not significant (lowercase letters). Each bar in panel (d) provides a summary of the effect of one of the three ecophysiological traits addressed (Sub-models I-III) on restricting the advancing of spring phenology under a warming climate: the higher the mean value shown, the stronger the restricting effect.

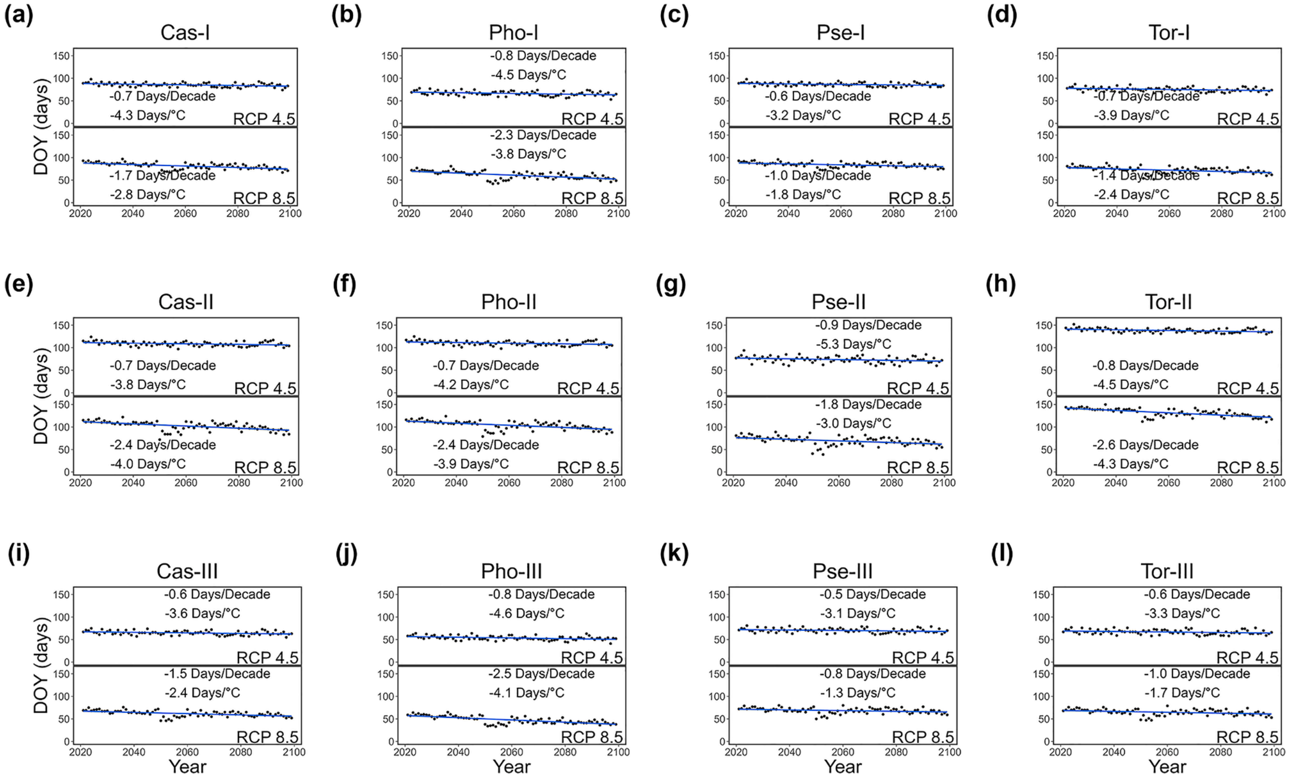

Fig. 7. Projected timing of the spring phenology in twelve Theoretical Tree Genotypes (TTGs) in Hangzhou, south-eastern China, for 2020 – 2100 under the climatic scenarios RCP4.5 and RCP8.5. For the TTGs, the process-based tree phenology model of *Torreya* flowering (Fig. 3, dashed lines in Fig. 2) was used, except that out of the three sub-models, one sub-model at a time was replaced with the corresponding sub-model developed for the leaf-out in the vegetative buds of one of the four tree species examined (solid lines in Fig. 2). The species is indicated by a three-letter abbreviation in the name of the TTG above each panel, with the Roman numeral indicating the replaced sub-model (Table S1).

temperatures (Baumgarten et al., 2021: R. Zhang et al., 2021, H. 2022) has a different answer for different tree species and bud types; and as shown by our simulation results (Fig. 6a), this difference may have major implications for the spring phenology of trees under climate warming. The differences between the five response curves shown in Fig. (2a) also show that any comparison between the chilling requirements of different species and bud types is temperature-dependant. For instance, when measured at +5 °C, the rate of rest break is the highest in *Torreya* flower buds (Fig. 2a), indicating that the chilling requirement, i.e., the time required for rest completion (Fig. S4), is the lowest in *Torreya* flower buds. Towards higher temperatures, however, this is reversed (Fig. 2a), indicating that at +14 °C, for instance, the chilling requirement is the highest in *Torreya* flower buds.

Second, the forcing effect of high temperatures on ontogenetic development is often approximated by applying the Growing Degree Days, which assumes a linear increase of the rate of development above a specific threshold (Chuine et al., 2013; Hänninen, 2016). However, experimental studies have shown that the real physiological air temperature response is non-linear (Sarvas, 1972; Caffarra et al., 2011) and that it varies between species (Caffarra and Donnelly, 2011; Zhang et al., 2022). Our study highlighted the crucial importance of the non-linearity and the inter-specific variability of the response for the effects of climate warming on the spring phenology of trees in subtropical conditions (Figs. 6b, d). This is in line with Hänninen (2006), who found this response to be critical for risk of tree frost damage under climate warming in boreal conditions.

Third, our results show that the classical division of the bi-phase process-based tree phenology models into the sequential and the parallel model (Hänninen, 2016) is an oversimplification (see also Chuine, 2000). Rather than a dichotomy, this phenomenon forms a continuum *in natura*, so that intermediate models are needed between the two extremes (Figs. 2c, S2). At one end of the continuum there is the sequential model, where no accumulation of forcing units (no ontogenetic development) takes place before the chilling requirement of rest completion is met ($C_o = 0$, Fig. S2a). At the other end there is the parallel model, where the accumulation of chilling gradually increases the accumulation rate of forcing units in any given forcing temperature (gradually increasing ontogenetic competence, C_o, Fig. S2a). Thus rest is deeper according to the sequential than the parallel model (Fig. S3). In our study the parallel model was found to adequately represent the vegetative buds of *Castanopsis* and *Phoebe* (Figs. 2c, S2a). For the vegetative buds of *Pseudolarix* and *Torreya* and the flower buds of *Torreya* trees, however, an intermediate model is needed (Figs. 2c, S2b). Furthermore, there were considerable differences between the latter three cases, as the vegetative buds of both *Pseudolarix* and *Torreya* (Fig. 2c) were near the parallel end of the continuum (Fig. S2b), whereas the flower buds of *Torreya* (Fig. 2c) were near the sequential end (Fig. S2b). Thus, as this third ecophysiological dormancy trait, the depth of dormancy, was also found to be critical for the projected effects of climatic change (Fig. 6c, Table 1), one should not fix the modelling *a priori* to either extreme of the continuum, i.e., the sequential or the parallel model. Rather, the real restrictions imposed by the rest status of the bud on the ontogenetic development, i.e., the real form of Sub-model III, should be determined experimentally.

4. Conclusions

Our results, when considered in the context of the pitfalls of straightforward inverse modelling based on observational data as documented in several earlier studies (Hunter and Lechowicz, 1992; Hänninen et al., 2019), highlight the need for time-consuming experimental work in the development of process-based tree phenology models for use in climate change impact assessments. There is no shortcut for biologically realistic process-based models of tree phenology. The good news is that for the purposes of climatic change impact assessments it is not necessary to delve into all the molecular details of the dormancy mechanisms involved (Cooke et al., 2012; Singh et al., 2017; Tylewicz et al., 2018). It suffices to address the three ecophysiological responses pinpointed in the modelling framework applied in the present study. Even this is obviously not feasible for all extratropical tree species addressed in global change research. Thus a balanced research strategy comprising both experimental (Zhang et al., 2022) and observational (Zhang et al., 2022) approaches is needed for the use of process-based tree phenology models in climatic change impact assessments.

Author contributions

RZ, HH and JW designed the study. JL and RZ performed the experiments. RZ, JL, JZ and HH performed the data analysis and modelling. RZ and JL wrote the first draft of the manuscript with inputs from HH and JW. The manuscript was rewritten several times on the basis of comments from IC, ND, IJ and KR.

Data availability

The original data is available upon request from the corresponding author.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:…

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2023.109593.

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