

# Sensitivity analysis of tree phenology models reveals increasing sensitivity of their predictions to winter chilling temperature and photoperiod with warming climate

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## ABSTRACT

The phenology of plants is a major driver of agro-ecosystem processes and biosphere feedbacks to the climate system. Phenology models are classically used in ecology and agronomy to project future phenological changes. With our increasing understanding of the environmental cues affecting bud development, phenology models also increase in complexity. But, we expect these cues, and the underlying physiological processes, to have varying influence on bud break date predictions depending on the specific weather patterns in winter and spring. Here, we evaluated the parameter sensitivity of state-of-the-art process-based phenology models that have been widely used to predict forest tree species phenology. We used sensitivity analysis to compare the behavior of models with increasing complexity under specific climatic conditions. We thus assessed whether the influence of the parameters and modeled processes on predictions varies with winter and spring temperatures. We found that the prediction of the bud break date was mainly affected by the response to forcing temperature under current climatic conditions. However, the impact of the parameters driving the response to chilling temperatures and to photoperiod on the prediction of the models increased with warmer winter and spring temperatures. Interaction effects between parameters played an important role on the prediction of models, especially for the most complex models, but did not affect the relative influence of parameters on bud break dates. Our results highlighted that a stronger focus should be given to the characterization of the reaction norms to both forcing and chilling temperature to predict accurately bud break dates in a larger range of climatic conditions and evaluate the evolutionary potential of phenological traits with climate change.

## 1. Introduction

Bud break is a key phenological event that affects plant performance by defining the period during which plants are able to grow, photosynthesize and produce their seeds. Therefore, the phenology of plants is a major driver of agro-ecosystem processes (Cleland et al., 2007) and biosphere feedbacks to the climate system (Richardson et al., 2013). It drives ecosystem productivity (Richardson et al., 2012), carbon (Delpierre et al., 2009), water (Hogg et al., 2000) and nutrient (Cooke and Weih, 2005) cycling processes, as well as energy balance (Wilson and Baldocchi, 2000). Moreover, plant phenology critically affects yield and organoleptic quality of crop harvest (Nissanka et al., 2015) as well as species distributions (Chuine, 2010). The onset of plant activity has been reported to advance by 2.5 days per decade on average during the

last 50 years (Menzel et al., 2006), potentially increasing the risk of frost damages on flowers and leaves (Vitasse et al., 2018a). These rapid responses have been shown to be highly species-specific and are expected to have major consequences on species interactions, species distributions, ecosystem functioning and forest carbon uptake (Cleland et al., 2007; Chuine, 2010; Richardson et al., 2013). Therefore, accurately predicting plant species phenology at both large and local scales is of key importance for assessing the impact of global change on agro-ecosystems and the multiple services they provide, as well as species range shift and populations' local extinction.

Fu et al. (2015b) showed however that the linear trend towards earlier spring onset had been slowing down significantly during the last two decades. One of the hypotheses put forward by the authors to explain this slowdown is the warming of winters. And indeed, recently,

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Asse et al. (2018) documented the negative effect of the warming of winter on the leaf unfolding and flowering date of several tree species. Air temperature is the major environmental factor regulating the dates of budburst and flowering of plants (Rathcke and Lacey, 1985; Polgar and Primack, 2011). In perennial species, temperature has an antagonistic effect on bud development depending on the season: low temperature (called chilling) are required to release the endodormancy of buds during winter, which is characterized by the inability of bud cells to grow despite optimal growing conditions, while higher temperature (called forcing) are required to promote bud cell elongation in spring. Recently, the effect of long photoperiod in compensating the lack of chilling temperature has also been reported for some tree species (Laube et al., 2014; Way and Montgomery, 2015; Zohner et al., 2016).

Our understanding of the environmental cues affecting species-specific bud break dates has been increasing thanks to the compilation of large phenological datasets (Menzel et al., 2006; Fu et al., 2015b), and to experimental work in controlled conditions using growth chambers (e.g. Caffarra and Donnelly, 2011; Zohner et al., 2016). This empirical knowledge has been essential for the development and calibration of process-based phenology models (Chuine and Regniere, 2017), that are used to predict spring phenology over large spatial and temporal scales (e.g. Chuine et al., 2016; Gauzere et al., 2017). While the relative contribution of environmental cues in driving spring phenological responses in current and future climatic conditions is still debated for most species (Chuine and Regniere, 2017; Laube et al., 2014; Fu et al., 2015a,b), the recent declining of the response of spring onset to global warming suggests that the relative influence of environmental cues driving the endodormancy phase varies with climatic conditions. Since climate change is likely to generate non-equilibrium conditions, the relative influence of the environmental cues might also not remain constant over time. Overall, a strong expectation is that the environmental cues releasing endodormancy should have an increasing influence in warmer environmental conditions. Yet, comprehensive analysis of the behavior of phenology models in different climates are still lacking, while pioneer modeling studies in crops have shown that it is expected to change depending on ecological conditions (e.g. Yin et al., 2005; Zhang et al., 2014).

Recently, Huber et al. (2018) highlighted the importance of improving our understanding of models behavior, and identifying key parameters and processes that have the strongest effects on model predictions under different ecological conditions. It is a major stage to enhance model applications across large spatial and temporal scales, as well as the robustness of model projections. We embrace this view and acknowledge here the usefulness of sensitivity analysis to reach this general objective. Sensitivity analyses are interesting statistical tools to address the impact of parameters variations on the outputs of models (Cariboni et al., 2007), allowing to evaluate both intrinsic (i.e. model structure and parameters) and extrinsic (i.e. model inputs) sources of variation. They can also highlight model limitations and directions for further improvements (Saltelli et al., 2000; Cariboni et al., 2007). Therefore, they represent an important step in the modeling cycle (Saltelli et al., 2000; Cariboni et al., 2007; Augusiak et al., 2014; Courbaud et al., 2015).

For forest tree species, most studies in phenology modeling have focused on the analysis of extrinsic sources of variation, e.g. investigating the uncertainty of climatic inputs on simulations (Morin and Chuine, 2005; Migliavacca et al., 2012). Ecological studies interested in intrinsic sources of variation most often evaluate the effect of the variation of single parameters on the model outputs, other parameters remaining fixed at a given default value (e.g. Lange et al., 2016). The major disadvantage of this approach is to neglect possible interactions among parameters and to be unreliable in presence of non-linear relationships between the parameters and the model predictions (Coutts and Yokomizo, 2014). At the opposite, sensitivity analyses varying all parameters simultaneously allow to account for parameter interactions and non-linear relationships and providing robust sensitivity measures

for complex simulation models. While phenology model complexity is increasing with our understanding of the physiological responses involved in bud development, these interaction effects and non-linear relationships can no more be overlooked. A first originality and aim of this study was thus to compare the behavior of phenology models with increasing complexity, and to disentangle the main and interaction effects of parameters on bud break date predictions.

The most commonly used phenology models are process-based, meaning that they describe known or suspected cause–effect relationships between physiological processes and some driving factors in the organism's environment to predict the precise occurrence in time of various phenology events (see for review Chuine and Regniere, 2017). The parameters of these models are either defined using parameter values measured in experimental controlled conditions, or statistically inferred from phenological and meteorological data using inverse modeling techniques. Since they describe causal relationships derived from experimental work, the sensitivity analysis of process-based models is supposed to reflect the sensitivity of the real processes (Saltelli et al., 2000). Therefore, we can expect the sensitivity of phenology models to specific parameters, e.g. driving the endodormancy phase, to change with varying climatic conditions. The impact of climate on observed and simulated bud break dates is expected to be complex, because of the cumulative and antagonistic effects of temperature depending on the season on bud development (Chuine and Regniere, 2017). For this reason, we also aimed at testing the parameter sensitivity of phenology models to climatic conditions. We thus analyzed model behavior under specific patterns of winter and spring temperatures, that produced either particularly early or late bud break date. This study thus differ from that of Lange et al. (2016) which explored the behavior of phenology models in uniformly warmer or colder conditions all along the year. In the present study we used different observed climatically contrasted years with their specific weather patterns.

Using a sensitivity analysis approach, we aimed at evaluating the parameter sensitivity of state-of-the-art process-based phenology models that have been widely used to predict bud break dates of forest tree species. The main originalities of this study are to (i) compare the behavior of models with increasing complexity; and, (ii) perform this analysis under realistic and contrasted climatic conditions in order to better estimate how the relative influence of parameters on model prediction varies with specific weather patterns in winter and spring. To perform this study we used historical climatic conditions encountered at different elevations in the Pyrenees Mountains, to cover a large range of temperature variation, without variation of the day length between sites. More specifically, we propose here to: (1) evaluate whether increasing model complexity is related to higher interaction effects between parameters; (2) identify key parameters and processes that cause the highest variability in the output of the models under different climatic regimes; (3) assess the physiological plausibility of this sensitivity; (4) discuss our outcome for future studies that will use phenology models to address key question in ecology and evolution. In particular, we expect parameters related to physiological responses to spring forcing temperatures to have a stronger impact on the prediction of the bud break date in cold environmental conditions, and more generally in historical climatic conditions in Western Europe. On the opposite, we expect parameters related to endodormancy release (requiring chilling conditions during winter) to have an increasing influence on the prediction of models in warmer environmental conditions. Finally, we expect parameter interactions to have a greater influence on the prediction of models with increasing model complexity.

## 2. Material and methods

### 2.1. Process-based phenology models

Process-based phenology models (see for review Chuine and

Regniere, 2017) are deeply grounded on experimental results which have accumulated over the last 50 years and describe how the development of buds, from dormancy induction in fall to bud break in spring, is determined by the individual or interactive effects of different environmental cues, notably temperature and photoperiod. Most of these models are based on the same framework (see Chuine and Regniere, 2017). Each development phase (e.g. endodormancy, ecodormancy) is described by a submodel determining its reaction norms to various cues. Several response functions describing the reaction norms to various cues can combine by addition, multiplication, or composition. Development phases either are sequential (follow each other in time) or overlap (a phase can start before the end of the previous one).

We chose three different kinds of model within this framework that represent the three main types of environmental regulation of bud break (of either vegetative or reproductive buds) in perennial species and are the most widely used in phenology studies: UniForc (Chuine, 2000), UniChill (Chuine, 2000) and PGC (Gauzere et al., 2017). These models differ by their complexity and by the environmental cues they account for. While UniForc and UniChill are thermal ecodormancy and endo-ecodormancy models respectively, PGC is a photothermal endo-ecodormancy model. In the three models described below,  $t_0$  defines the beginning of the endo- or ecodormant phase depending on the model,  $t_f$  the bud break date and  $F^*$  the critical amount of forcing units to reach bud break.

**NULL** – The UniForc model is an one-phase model, describing the cumulative effect of forcing temperatures on the development of buds during the ecodormancy phase. This model thus assumes that the endodormancy phase is always fully released and that there is no dynamic effects of chilling and photoperiod on forcing requirements. Bud break occurs when the rate of forcing,  $R_f$  (Eq. (7)), accumulated since  $t_0$ , reaches the critical state of forcing  $F^*$ :

$$\sum_{t_0}^{t_f} R_f(T) \geq F^* \quad (1)$$

with  $T$ , the daily average temperature.

**UNICHILL** – The UniChill model is a sequential two-phases model describing the cumulative effect of chilling temperatures on the development of buds during the endodormancy phase (first phase) and the cumulative effect of forcing temperatures during the ecodormancy phase. Like in the UniForc model, bud break occurs when the accumulated rate of forcing,  $R_f$ , reaches  $F^*$  (Eq. (1)). The start of the ecodormancy phase corresponds to the end of the endodormancy phase,  $t_c$ , which occurs when the accumulated rate of chilling  $R_c$  (Eq. (8)) has reached the critical state of chilling  $C^*$ :

$$\sum_{t_0}^{t_c} R_c(T) \geq C^* \quad (2)$$

**PGC** – The PGC model has been designed to explain bud break date of photosensitive species, which might represent about 30% of the species (Zohner et al., 2016). It has been shown to be particular relevant to simulate the bud break date of beech (*Fagus sylvatica* L.) which is one of the most photosensitive species for bud break (Gauzere et al., 2017). This is a photothermal model that integrates the compensatory effect of photoperiod on insufficient chilling accumulation through a growth competence function (GC; Gauzere et al., 2017). The growth competence function describes the ability of buds to respond to forcing temperatures. It modulates the rate of forcing ( $R_f$ ) through a multiplicative function to define the actual daily forcing units accumulated by the bud until bud break as:

$$\sum_{t_0}^{t_f} (GC(P)R_f(T)) \geq F^* \quad (3)$$

with  $P$  and  $T$ , the daily photoperiod and average temperature respectively.

The growth competence (GC) is related to the daily photoperiod through a sigmoid function:

$$GC(P) = \frac{1}{1 + e^{-d_p(P-P_{50}(t))}} \quad (4)$$

with  $P_{50}$ , the mid-response photoperiod and  $d_p$ , the positive slope of the sigmoid function.

$P_{50}$  is not constant and depends on the state of chilling (CS): the greater the accumulated rate of chilling, the shorter the mid-response photoperiod, i.e. buds become sensitive to shorter photoperiod when they have accumulated chilling:

$$P_{50}(CS) = (12 - P_r) + \frac{2P_r}{1 + e^{-d_c(CS(t)-C_{50})}} \quad (5)$$

with  $P_r$ , the range boundaries of the parameter  $P_{50}$ , so that  $P_{50} \in [12 - P_r; 12 + P_r]$ ,  $d_c$  the negative slope of the sigmoid function, and  $C_{50}$  is the mid-response parameter if the sigmoid function, reflecting chilling requirements under short-day length. Finally, chilling units accumulated as:

$$CS(t) = \sum_{t_0}^t R_c(T) \quad (6)$$

For the sake of comparison, the version of the models used for this study have the same type of response functions to forcing and to chilling temperatures. The response function to forcing temperature,  $R_f$ , was defined as a sigmoid function as it has been shown to be the most realistic experimentally (Hanninen et al., 1990; Caffarra and Donnelly, 2011):

$$R_f(T_d) = \frac{1}{1 + e^{-d_T(T_d-T_{50})}} \quad (7)$$

with  $d_T$ , the positive slope and  $T_{50}$ , the mid-response temperature of the sigmoid function. We defined the rate of chilling,  $R_c$ , as a threshold function (Caffarra et al., 2011b):

$$R_c(T_d) = \begin{cases} 1 & \text{if } T_d < T_b \\ 0 & \text{if } T_d \geq T_b \end{cases} \quad (8)$$

with  $T_b$ , the mean temperature of day  $d$  and  $T_b$ , the threshold temperature (also called base temperature) of the function.

As defined here, the UniForc model has 4 parameters ( $t_0$ ,  $d_T$ ,  $T_{50}$ ,  $F^*$ ), the UniChill model 6 parameters ( $t_0$ ,  $T_b$ ,  $C^*$ ,  $d_T$ ,  $T_{50}$ ,  $F^*$ ), the PGC model 9 parameters ( $t_0$ ,  $T_b$ ,  $C_{50}$ ,  $P_r$ ,  $d_c$ ,  $d_p$ ,  $d_T$ ,  $T_{50}$ ,  $F^*$ ; Table 1).

## 2.2. Model calibration and validation

In order to set up the sensitivity analysis design, we first calibrated and validated the studied phenology models for three emblematic tree species in European forests: common beech (*F. sylvatica*), sessile oak (*Quercus petraea* L.) and silver fir (*Abies alba* Mill.). These results were used to (i) define the natural parameter variation among tree species (Table 1) and (ii) identify contemporary climatic years that produced particularly early and late spring phenology (Appendix 4). The three models were parametrized for the three different species using observations of the bud break date in the Pyrenees and corresponding weather data from 2005 to 2012.

The phenology of several populations located at different elevations following the Gave and Ossau valleys in the Pyrenees have been yearly monitored since 2005. The studied populations ranged from 131 to 1604 m (9 sites) for beech, from 131 to 1630 m (13 sites) for oak, and from 840 to 1604 m (6 sites) for fir (for further details about these populations, see Vitasse et al., 2009). Data used for this study consisted in the bud break date (BBCH 9) monitored from 2005 to 2012 in these populations. Models were parametrized using daily weather data since 2004 from Prosensor HOBO Pro (RH/Temp, Onset Computer Corporation, Bourne, MA 02532) that have been placed at the core of each monitored population (Vitasse et al., 2009). Day length was calculated

**Table 1**

Description and sampling distribution of the parameters of the three models used to perform the sensitivity analysis. For all parameters, except slope parameters, values were drawn in uniform distributions  $\mathcal{U}$ . For slope parameters  $d$ , values were drawn in beta distributions  $\mathcal{B}_{\{\alpha=20;\beta=1.3\}}$ . The species parameter range provides the variation range of the adjusted parameters for three major European tree species (*F. sylvatica*, *Q. petraea*, *A. alba*). More details about the sampling distributions choices, based on the model calibration and the empirical knowledge of about the physiological responses, are provided in Appendix 5). DOY = day of the year; DU = developmental units; DR = developmental rate.

Parameter	Models	Description	Units	Species parameter range	Sampling distribution
$t_0$	UniForc	Starting date of ecodormancy	DOY	[22; 90]	$\mathcal{U}$ [−31; 92]
$t_0$	UniChill, PGC	Starting date of endodormancy	DOY	[−120; −62]	$\mathcal{U}$ [−122; −31]
$F^*$	UniForc, UniChill, PGC	Critical state of forcing	DU	[16.3; 106.8]	$\mathcal{U}$ [1; 30]
$T_{50}$	UniForc, UniChill, PGC	Mid-response temperature to forcing	°C	[2.8; 15.7]	$\mathcal{U}$ [0; 14]
$d_r$	UniForc, UniChill, PGC	Slope of the forcing response	DR/°C	[0.051; 0.44]	$\mathcal{B}_{\{\alpha=20;\beta=1.3\}}$
$C^*$	UniChill	Critical state of chilling	DU	[1.1; 116.7]	$\mathcal{U}$ [1; 60]
$T_b$	UniChill, PGC	Threshold chilling temperature	°C	[10.7; 14.9]	$\mathcal{U}$ [7; 13]
$C_{50}$	PGC	Mid-response parameter of the photoperiod sensitivity	DU	[5.7; 192.3]	$\mathcal{U}$ [1; 60]
$P_r$	PGC	Range boundaries of the mid-response photoperiod	h	[0.9; 1.5]	$\mathcal{U}$ [1; 6]
$d_c$	PGC	Slope of photoperiod sensitivity response	h/units	[−40; −0.64]	$\mathcal{B}_{\{\alpha=20;\beta=1.3\}}$ [−10; −10 <sup>−5</sup> ]
$d_p$	PGC	Slope of the growth competence	DR/h	[0.26; 11.9]	$\mathcal{B}_{\{\alpha=20;\beta=1.3\}}$ [10 <sup>−5</sup> ; 10]

according to the latitude of the meteorological stations (see Caffarra et al., 2011a). Using these datasets, the three studied models were parametrized for each species following Gauzere et al. (2017). The models RMSE varied from 5.85 to 10 days, with mean RMSE of 6.28 for beech, 6.92 for oak, 9.39 for fir (Appendix 3).

### 2.3. Sensitivity analysis

To perform the sensitivity analysis we sampled 1,000,000 parameters combinations for each model, to fully capture each parameter space. To sample each parameter, we used beta distributions for the slope parameter of the sigmoid functions (Eqs. (4), (5) and (7)) and uniform distributions for other parameters (Appendix 5). The beta distribution was chosen to account for the fact that variations in shape parameters have differential effects on sigmoid responses (variation in extreme shape values have a lowest impact on the global shape of the sigmoid function). The bounds of the sampling distributions were defined according to two criteria: (i) the sampled values needed to be biologically relevant, i.e. make sense according to the empirical knowledge about the physiological responses and the adjusted values for the three species, and (ii) produce positioned dates, i.e. dates different from the last day of the year (DOY  $\neq$  365). Due to these constraints, all parameters do not have the same variance (coefficient of variation ranging from 0.05 to 0.18). Appendix 5 details the parameter values adjusted for each species in the parameter space explored for the sensitivity analysis.

Two different sensitivity indexes, describing the proportion of variance of the model's output  $Y$  (here bud break date) explained by the variation of a given parameter  $X_i$ , were calculated from the “Sobol” and “Sobol–Jansen” methods implemented in the package “sensitivity” of the R software. These two methods implement the Monte Carlo estimation of the variance-based method for sensitivity analysis proposed by Sobol (1993). More precisely, these functions allow estimating the first-order and total-effect indexes from the variance decomposition, sometimes referred to as functional ANOVA decomposition. The first-order index is defined as:

$$S_i = \frac{\text{Var}_{X_i}(E_{X \sim i}(Y|X_i))}{\text{Var}(Y)} \quad (9)$$

with

$$\sum_{i=1}^n S_i = 1 \quad (S_i > 0) \quad (10)$$

$Y$  is the prediction and  $X_i$  is the  $i$ th parameter of the model. The notation ( $X \sim i$ ) indicates the set of all variables except  $X_i$ . The numerator represents the contribution of the main effect of  $X_i$  to the variation in

the output, i.e. the effect of varying  $X_i$  alone, but averaged over variations in other input parameters.  $S_i$  is standardized by the total variance to provide the fractional contribution of each parameter  $i$ .

And total-effect index as:

$$S_{Ti} = \frac{E_{X \sim i}(\text{Var}_{X_i}(Y|X_{\sim i}))}{\text{Var}(Y)} = 1 - \frac{\text{Var}_{X \sim i}(E_{X_i}(Y|X_{\sim i}))}{\text{Var}(Y)} \quad (11)$$

with

$$\sum_{i=1}^n S_{Ti} \geq 1 \quad (S_{Ti} > 0) \quad (12)$$

due to the interaction effect, e.g.  $X_i$  and  $X_j$  both counted in  $S_{Ti}$  and  $S_{Tj}$ .  $S_{Ti}$  thus measures the contribution of  $X_i$  to the variation in the output, including all variances caused by its interactions with any other input variables.

### 2.4. Climatic data used for the sensitivity analysis

To perform the sensitivity analysis, we used the climate simulated at different elevations, over a gradient of 1000 m, for the period from 1956 to 2012, in order to explore a large range of climatic conditions. To study the response of the models to realistic climate at different elevations, we used measurements taken with local weather stations on three forest sites, at 627, 1082 and 1630 m a.s.l., along the Gave valley (Prosensar HOBOPRO; Vitasse et al., 2009). As this weather dataset only covered the period from 2004 to 2012, we also used Météo France measurements at other stations located close to these sites, and data from the SAFRAN reanalysis on the points of the systematic grid located in the valley, to simulate the climate at the forest sites over a larger period (1959–2012). The temperature data recorded with the local HOBOPRO sensors were linearly correlated to the climatic data derived by the SAFRAN model of Météo France (Quintana-Segui et al., 2008) for the same period. Daily minimum and maximum temperature data from 1960 to 2012 were generated based on the long-term SAFRAN outputs using the following equation:

$$T(X) = \beta_i(X) + \alpha_i(X). T_{\text{SAFRAN}} \quad (13)$$

with  $X$ , the targeted site;  $\beta_i$  and  $\alpha_i$ , the intercept and the slope of the linear regression between  $T_{\text{SAFRAN}}$  and  $T_{\text{HOBOPRO}}$  for the period 2004–2012. The coefficients used for this equation are provided in Appendix 1. Day length was calculated according to the latitude of the forest sites (see Caffarra et al., 2011a).

Over this large simulated period, we chose three climatically contrasted years, that corresponded to (1) a year with winter and spring mean temperatures close to their global mean over the 1960–2012 period (“normal climatic year”; year 1966), (2) a year expected to



**Table 2**

Detail of the climatic conditions used to perform the sensitivity analysis of the phenological models. With  $T_{NovDec}$ , the average temperature of November and December of the previous year (in °C);  $T_{JanFeb}$ , the average temperature of January and February of the focal year (in °C) and  $T_{MarAprMay}$ , the average temperature of March, April and May of the focal year (in °C).

Elevation	Year	$T_{NovDec}$	$T_{JanFeb}$	$T_{MarAprMay}$
627 m	1966	7.18	6.37	11.45
	1975	8.97	7.46	10.23
	2011	5.72	6.99	14.52
1082 m	1966	5.85	5.12	9.44
	1975	7.42	6.018	8.40
	2011	4.64	5.72	12.02
1630 m	1966	3.20	2.50	6.54
	1975	4.67	3.33	5.56
	2011	2.07	3.07	8.94

produce early spring phenology, i.e. with cooler winter and warmer spring temperatures than normal (“early climatic year”; year 2011) and (3) a year expected to produce late spring phenology, i.e. with warmer winter and cooler spring temperatures than normal (“late climatic year”; year 1975; Table 2; Appendix 2). We checked that the three years selected indeed generated early, average and late bud break dates using the adjusted models for different tree species (Appendix 4). This range of climatic conditions allowed us to credibly investigate the impact of specific weather patterns in winter and spring on the behavior of the models.

### 3. Results

#### 3.1. Main trends in parameter sensitivity of phenology models

For the three models, the mid-response temperature during the ecodormancy ( $T_{50}$ ) had the greatest influence on the predictions of the models in most of the climatic conditions explored, except in the cool winter-warm spring conditions producing early phenology (Fig. 1, and see Appendices 6, 7 and 8 for detailed results). This strong influence is both due to the main effect of  $T_{50}$  and its interaction with other parameters, and especially with  $d_T$ ,  $T_{50} \times d_T$  defining the shape of the forcing response during the ecodormancy phase. Under the conditions producing early phenology, the main parameters affecting the predicted bud break date were  $t_0$ ,  $T_{50}$  and  $F^*$  for UniForc, UniChill and PGC respectively (Fig. 1a). Note that the influence of the parameters on the predictions of the models was significantly affected by their coefficient of variation (i.e. parameters that had the highest variation also had the highest influence; Fig. 2). However, this effect only explained a small proportion of the total variation in the total-effect of the parameters ( $R^2 = 0.29$ ).

#### 3.2. The sensitivity to model parameters varies with model complexity

The sensitivity of model predictions to the variation in model parameters highly depended on the phases and processes modeled (Fig. 1). Predictions of the ecodormancy model UniForc were more sensitive to the  $t_0$  parameter, i.e. the model starting date, than the predictions of the endo-ecodormancy models UniChill and PGC, particularly under the climatic conditions producing early phenology (Fig. 1a and b). Predictions of the thermal model UniChill were more sensitive to the critical amount of chilling to release dormancy ( $C^*$  parameter) than the predictions of the photothermal model PGC to the equivalent parameter ( $C_{50}$ ). Predictions of this latter photothermal model was more sensitive to the critical amount of forcing ( $F^*$ ) than that of the thermal models UniForc and UniChill. Finally, predictions of the UniChill model were more sensitive to the mid-response temperature during ecodormancy ( $T_{50}$ ) than that of the UniForc and PGC models, which presented similar sensitivity to this parameter (Fig. 1).

Depending on the model complexity, the uncertainty in the predictions will thus reply in the accurate calibration of different key parameters.

#### 3.3. The sensitivity to model parameters varies with climate

The sensitivity of the model predictions to the variation in model parameters also changed according to the climatic conditions experienced during winter and spring (Fig. 3). In the three models, the sensitivity of the predictions to the mid-response temperature during ecodormancy ( $T_{50}$ ) decreased with warming temperature (Fig. 3), while the sensitivity to the parameters driving the endodormancy phase (e.g.  $t_0$  in the UniForc model,  $C^*$  in the UniChill model,  $d_p$  and  $C_{50}$  in the PGC model) increased with warming temperature (Fig. 3). The sensitivity of the endo-ecodormancy models to the critical amount of forcing to reach bud break ( $F^*$ ) was also higher in warmer conditions. This is probably because, even if forcing accumulation becomes less limiting with warming temperature,  $F^*$  still represents the minimum duration of the ecodormancy phase and thus strongly drives bud break date.

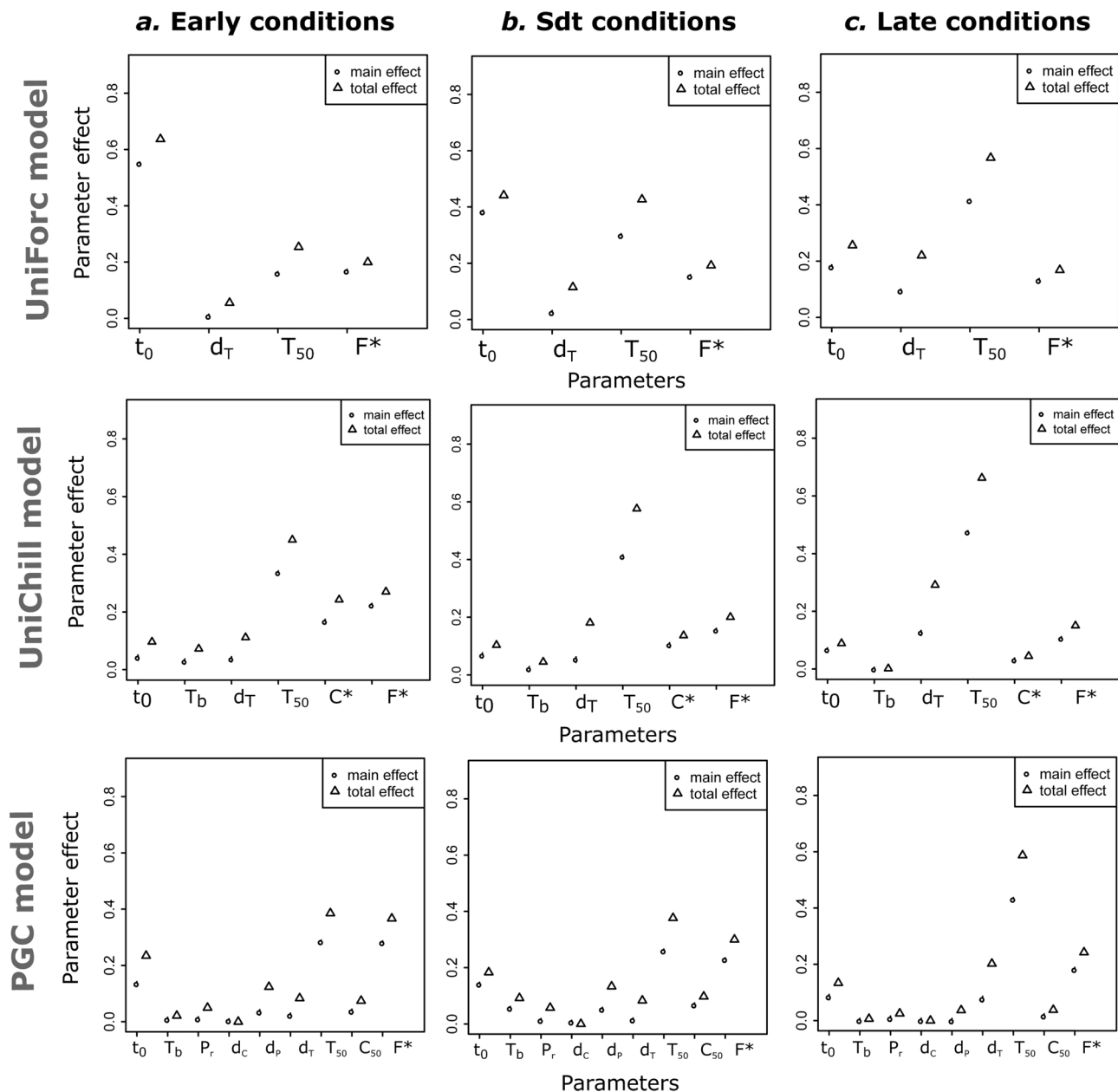
The sensitivity of the predictions of the PGC model to both the critical amount of chilling ( $C_{50}$ ) and the parameter determining the sensitivity to photoperiod ( $d_p$ ) increased with warming temperature (Fig. 3). But, in such conditions, the sensitivity of PGC model predictions to the photoperiod related parameter was higher than that to chilling related parameters ( $C_{50}$  and  $T_b$ ; Fig. 3). Finally, the sensitivity of PGC model predictions to the starting date of endodormancy ( $t_0$ ) tended to increase with warming temperature conditions, while that of the UniChill model remained constant and low (Fig. 3). This result may be explained by the differences in growth competence modeling between these two models. The growth competence function of the PGC model is not null in autumn but decreases with the decreasing day length, and induces endodormancy. If temperature conditions are particularly favorable, some forcing units can be accumulated before endodormancy is fully induced contrary to the UniChill model. This therefore gives an increasing importance to  $t_0$  in driving bud break dates in warmer temperature conditions.

For the three models, the increasing influence of the endodormancy vs ecodormancy related parameters on bud break date predictions can already be noticed in warm winter conditions.

#### 3.4. Main and interaction effects

In the results above, we describe the influence of the parameters on the predictions of the models based on their total effect, which include both main and second-order interaction effects. However, it is also interesting to decompose these effects to understand their relative contributions to the variation of bud break dates. For most parameters, the total effects were mainly due to main (or first-order) effects, and in a lesser extend to interaction effects between parameters (or second-order effects; Fig. 1). Second-order effects always explained less than 15% of the predictions variation (while the largest first-order effect explained more than 50% of the output variation; Fig. 4 and Appendix 9). Interestingly, interaction effects did not modify the relative influence of the parameters on the predictions of the models (Fig. 1). Nevertheless, total interaction effects represented an important source of variation in the predicted bud break dates (Fig. 4), in particular for the most complex models.

The total influence of interaction effects on model predictions also varied with the specific weather patterns in winter and spring. For UniForc, total interaction effects were found to be more important in the warm winter-cool spring conditions, producing late phenology, while for PGC, these effects were more important in the cool winter-warm spring conditions, producing early phenology (Fig. 4a and c). The interaction between the parameters  $T_{50}$  and  $d_T$  had the largest effect on the predicted bud break date, notably in the coldest temperature conditions ( $d_T \times T_{50}$ ; Appendix 9). These two parameters define the shape of the response to temperature during ecodormancy in the three



**Fig. 1.** Main and total effects of the parameters on the predictions of the three studied models in the most contrasted climatic conditions. The main effect (or first-order effect) quantifies the individual effect of a parameter, i.e. without interactions. The total effect represents the first- and second-order effects (i.e. with second-order interaction effects). These effects quantify the proportion of variance of the model's prediction explained by the variation of a given parameter. (a) “Early conditions” corresponds to climatic conditions at 627 m in 2011, producing the earliest phenology, (b) “standard conditions” to climatic conditions at 1082 m in 1966, producing intermediate phenology, and (c) “late conditions” to climatic conditions at 1603 m in 1975, producing the latest phenology over the range of conditions explored. The details of the results for each site and year are given in Appendix 8.

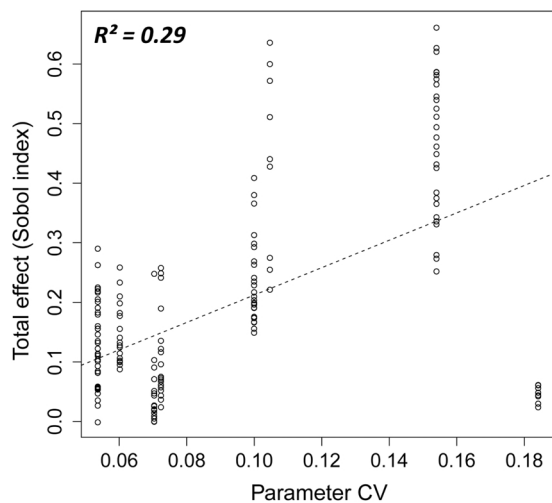
models. For the PGC model in the warmest climatic conditions, the interaction between the endodormancy starting date ( $t_0$ ) and the photoperiod sensitivity ( $d_p$ ) also had an impact on the predicted bud break date ( $t_0 \times d_p$ ; Appendix 9). The influence of interaction effects thus tended to increase with model complexity, but also varied with specific weather patterns in winter and spring.

#### 4. Discussion

##### 4.1. Bud break date predictions mainly depend on the forcing response under current climatic conditions

The sensitivity analysis of the studied process-based models showed

that the mid-response temperature of the ecodormancy phase (called here  $T_{50}$ ) plays a critical role in the prediction of bud break date under current climatic conditions. This result applies whether models account or not for an endodormancy phase or a photoperiodic control of bud development. It therefore suggests that the response to forcing temperature during the ecodormancy (defined by both  $T_{50}$  and  $d_T$  in the studied phenological models) is a major physiological response driving the variation of bud break dates in temperate plant species in historical and current climatic conditions. This finding is consistent with previous correlative modeling studies showing that bud break date variation was mainly driven by the mean temperature of the two preceding months, which roughly corresponds to the ecodormancy phase (e.g. Menzel et al., 2006). It is also consistent with previous process-based modeling



**Fig. 2.** Variation in the total-effect of parameters on the predictions of all models according to their coefficients of variation (CV). The coefficient of variation of each parameter was estimated from its sampling distribution. The  $R^2$ -squared was estimated using a linear model. The parameters with the highest CV were also the most influential on models prediction.

studies showing that models simulating only the ecodormancy phase explained as much variance in bud break dates as models simulating both the endo- and ecodormancy phases (Linkosalo et al., 2006; Gauzere et al., 2017). The similar performance of the two types of model suggested either that the fulfillment of chilling requirements had not been a limiting factor so far, or that the endodormancy phase is not accurately modeled (Linkosalo et al., 2006; Chuine et al., 2016). Our results support the first hypothesis, i.e. winter chilling temperature have played a minor role in bud break variations so far, which also explains why the response of plant species to climate warming has so far resulted in an advancement of the bud break dates (Menzel et al., 2006). A methodological consequence of this is that phenological records in natural populations may not allow estimating accurately endodormancy model parameters (Chuine et al., 2016).

#### 4.2. Bud break date predictions are increasingly dependent on chilling temperatures and photoperiod as climate warms

We found that the effect of the reaction norm to forcing temperature on the prediction of the bud break date decreased with warming spring conditions, while the effect of chilling accumulation during the endodormancy phase increased with warming winter temperature for the thermal endo-ecodormancy models UniChill and PGC. This suggests that in warmer environmental conditions reaction norms to temperature during both bud endodormancy and ecodormancy are critical in determining bud break dates. This result is supported by several recent experimental studies showing that temperature sensitivity of the bud break dates was currently decreasing, likely due to an increasing influence of warming winters on bud endodormancy (Fu et al., 2015a,b; Vitasse et al., 2018b; Asse et al., 2018). In particular, Vitasse et al. (2018b) showed that a differential response to chilling temperatures between trees living at low and high elevations may explain the difference in the temporal trends of bud break date advancement observed at different elevations with warming conditions during the last decade. Overall, these results highlight that the influence of chilling temperatures on bud development can no longer be overlooked, and that the correct estimation of the parameters governing the endodormancy phase is required to accurately predict bud break.

The sensitivity analysis of the photothermal endo-ecodormancy model PGC showed that the influence of the photoperiodic response (through the  $d_p$  parameter) on the prediction of the bud break date

increased in warmer environmental conditions. A growing number of studies suggest that the phenology of up to 30% of tree species might be sensitive to photoperiod at various degrees (Laube et al., 2014; Zohner et al., 2016). Understanding how this increasing effect of the photoperiodic cue will affect the variation of bud break dates in future climatic conditions is an issue still debated (Fu et al., 2015b; Gauzere et al., 2017). However, in the most sensitive species, such as beech, it has been suggested that this sensitivity may counteract the negative effect of insufficient chilling during winter (Gauzere et al., 2017). Our results thus highlight that a stronger focus should be given to the modeling of the reaction norm to photoperiod to be able to accurately predict bud break dates of up to 30% of tree species in future climatic conditions.

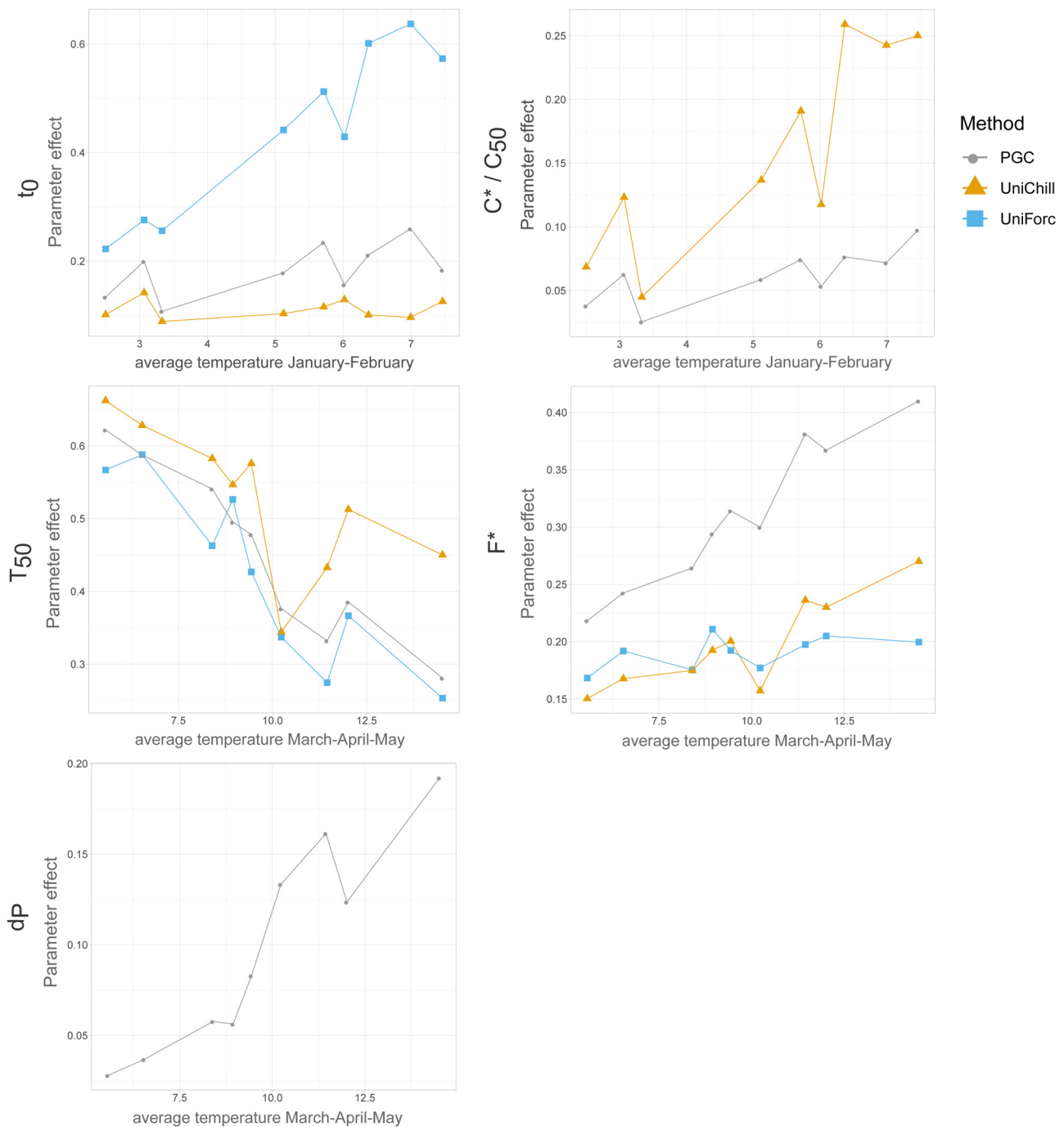
#### 4.3. Originality and limits of the study

Only a few studies have performed sensitivity analysis of phenology models so far. They either analyzed the behavior of phenology models, identified the main sources of uncertainties in bud break date predictions, or assessed the consequences of phenological uncertainties on related processes (e.g. Morin and Chuine, 2005; Migliavacca et al., 2012; Zhang et al., 2014; Lange et al., 2016). A key results from these previous studies is that uncertainty in climate conditions, notably generated by climate scenarios, was a greater source of variation in phenological date projections than uncertainty in phenology models (Migliavacca et al., 2012).

To our knowledge, this study is the first to have compared the behavior of different phenology models, with increasing complexity, and to perform this analysis under different weather patterns in winter and spring. The results found here are in line with a recent sensitivity analysis of species-specific phenology models, which found an increasing importance of chilling requirements and photoperiod in warm climatic conditions for temperate tree species (Lange et al., 2016). The consistency of our results with the sensitivity analysis of other phenology models strengthens the scope of our study, and thus further stress the importance of investigating the behavior of phenology models in contrasted climatic conditions in order to fully embrace their robustness.

While the climate we used to perform the sensitivity analyses covers a small geographical region, it still explores a large range of variation in winter and spring average temperatures ( $T_{NovDec} \in [2.07; 8.97]$ ,  $T_{MarAprMay} \in [5.56; 14.52]$ ). This temperature variation is less important than in other sensitivity analyses (e.g. Lange et al., 2016), but it is large enough to allow extrapolating the results of this study at larger spatial scales. The aim of the present study was not to investigate the behavior of phenology models under climate change scenarios. Nevertheless, by extrapolating our results on the impact of warming conditions on parameter sensitivity, we can expect the influence of the parameters governing the endodormancy to overall have more influence on bud break date predictions in the future.

Due to the high computational requirement of sensitivity analyses, most studies usually neglect, partially or completely, interaction effects between model parameters as a source of output variation (e.g. Lange et al., 2016). However, the complexity of process-based phenology models tends to increase as we gain better knowledge about the physiological processes involved in bud development. With increasing model complexity and realism, we can expect interaction effects to have non-negligible influence on the prediction of the models, and thus local sensitivity analysis to partially reveal the effect of parameters on output variance. Our results also suggest that model complexity would result in higher uncertainty in bud break dates because of interaction effects. Moreover, increasing model complexity would generate higher uncertainty in model outputs because of parameter compensation during the statistical adjustment, notably if models are used to perform predictions outside of the range of the climatic conditions used to adjust them (Gauzere et al., 2017).



**Fig. 3.** Variation in the total effect of the most biologically relevant parameters on the predictions of the three studied models according to climatic variables (see also Appendix 7). The total effect quantifies the proportion of variance in the model's prediction explained by the variation of a given parameter (considering its main and interaction effects). We chose to represent the average temperature of January and February because it is known to be involved in endodormancy release, and the average temperature of March, April and May because it is known to be involved in bud growth during ecodormancy. The climatic gradient corresponds to the nine contrasted climatic conditions used to perform the sensitivity analyses.

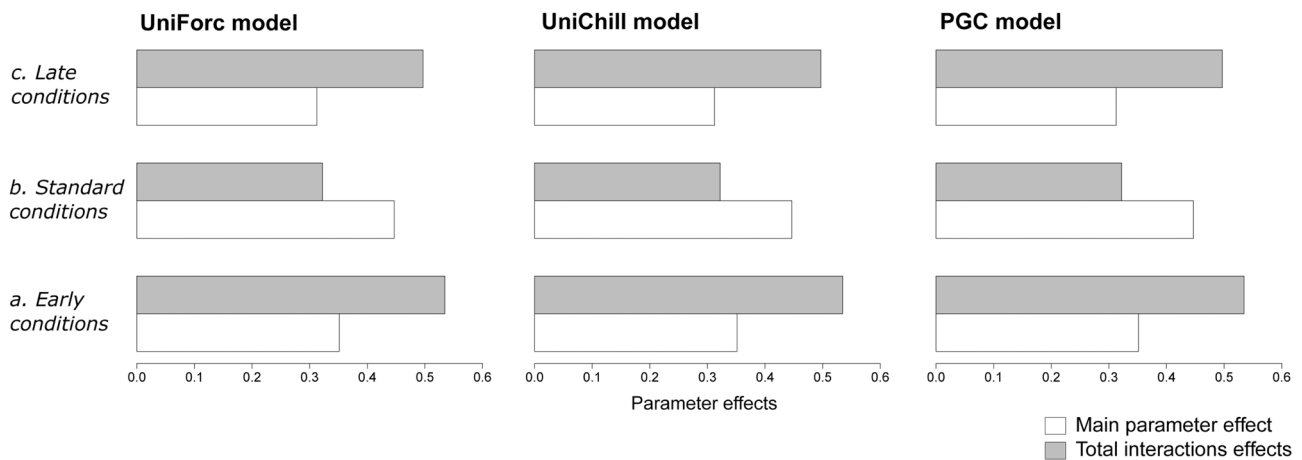
Here, we showed that sensitivity analysis of process-based phenology models are relevant to identify key parameters and processes that have the largest effect on phenology (Migliavacca et al., 2012; Lange et al., 2016). However, the choice of the parameter variation range likely affects the results of such analyses. Since for most plant species, the range limits or shape of the distributions of the physiological parameters in natural populations are unknown, such sensitivity analyses rely on assumptions that cannot be tested. Here, we might have overestimated the real contribution of  $T_{50}$  and  $F^*$  to the variation of the bud break date due to uneven variances in parameter sampling

distributions. This effect of parameter variation on the outcome of sensitivity analyses should be more acknowledged. To improve the scope and relevance of sensitivity analyses, more attention should be given to the characterization of the natural variation of the physiological parameters described in process-based models (e.g. Burghardt et al., 2015).

#### 4.4. Implications for the adaptive potential of phenological traits

While the sensitivity analysis of phenology models has direct





**Fig. 4.** Proportion of the variation in model predictions explained by the main individual parameter effect and the total interaction effect for each model under the three most contrasted climatic conditions. The main parameter individual effects is the proportion of variance in the predictions explained by the most influential parameter ( $T_{50}$  in most cases). The total interaction effects are the cumulative influence of the second-order interaction effects on models prediction. (a) “Early conditions” corresponds to climatic conditions at 627 m in 2011, (b) “standard conditions” to climatic conditions at 1082 m in 1966, and (c) “late conditions” to climatic conditions at 1603 m in 1975.

implications for ecological and climate change studies, we wanted to highlight also here their usefulness for evolutionary studies. The bud break date is among the most genetically differentiated trait across species distribution ranges (De Kort et al., 2013), suggesting that it is strongly involved in the process of local genetic adaptation. Evolutionary response of the bud break date is expected to depend on which parameters present genetic variation and how this variation impacts the bud break date, i.e. the expressed trait variation. Sensitivity analysis outputs can be used to address this second issue. For example, our results show that the mid-response temperature of the ecodormancy phase ( $T_{50}$ ) has the highest impact on the variation of the bud break date in most conditions. We thus suggest that future experimental research consider measuring the genetic variation of this key physiological trait in natural populations and crops to evaluate their adaptive potential. This can be done by monitoring bud break of several genotypes either in varying controlled conditions (e.g. Caffarra et al., 2011b), or by monitoring growth transcriptor factors in natura or in the field using new transcriptomic technics (e.g. Nagano et al., 2012), or even better by combining both approaches (e.g. Satake et al., 2013). Given the increasing importance of the response to chilling temperatures during the endodormancy phase to determine the bud break date in warming conditions, future experimental research might additionally consider measuring the genetic variation in chilling requirement and reaction norms to chilling temperature, especially in species requiring large amount of chilling. Finally, future experimental research should consider measuring the genetic variation in the reaction norm to photoperiod in most sensitive species, and notably beech (Goyne et al., 1989 for example in crops).

## 5. Conclusions

The identification of the physiological responses underlying the bud break date variation in current environmental conditions is an important on-going experimental research field (Fu et al., 2015a,b; Vitasse et al., 2018b). Assuming that process-based phenology models reflect real physiological responses and processes, the analysis of their behavior under contrasted climatic conditions can provide valuable information about this issue. Our results highlighted the major influence of the response to forcing temperature on the prediction of the bud break date, but also an increasing importance of the responses to chilling temperature and photoperiod in warming environmental conditions. Changes in the sensitivity of the prediction of phenology models to their parameters with climatic conditions highlights that we

need to better take into account the temporal and spatial variation of environmental conditions when analyzing phenological changes (Vitasse et al., 2018b). More generally, we acknowledge here that the sensitivity analysis of process-based models is a useful tool to understand the relative contributions of environmental cues in driving phenotypic traits variation and their evolutionary potential (Donohue et al., 2015; Burghardt et al., 2015; Lange et al., 2016).

## Conflict of interest

The authors have no conflict of interest to declare.

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## Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.ecolmodel.2019.108805>.

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