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**Title: 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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## 1 **Abstract**

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

22

23 **Key words:** Sensitivity analysis; Process-based modeling; Bud development; Forcing temper-  
24 ature; Chilling temperature; Photoperiod

## 25 **1 Introduction**

26 Bud break is a key phenological event that affects plant performance by defining the period  
27 during which plants are able to grow, photosynthesize and produce their seeds. Therefore, the  
28 phenology of plants is a major driver of agro-ecosystem processes (Cleland *et al.*, 2007) and  
29 biosphere feedbacks to the climate system (Richardson *et al.*, 2013). It drives ecosystem pro-  
30 ductivity (Richardson *et al.*, 2012), carbon (Delpierre *et al.*, 2009), water (Hogg *et al.*, 2000)  
31 and nutrient (Cooke & Weih, 2005) cycling processes, as well as energy balance (Wilson &  
32 Baldocchi, 2000). Moreover, plant phenology critically affects yield and organoleptic quality  
33 of crop harvest (Nissanka *et al.*, 2015) as well as species distributions (Chuine, 2010). The  
34 onset of plant activity has been reported to advance by 2.5 days per decade on average dur-  
35 ing the last 50 years (Menzel *et al.*, 2006), potentially increasing the risk of frost damages on  
36 flowers and leaves (Vitasse *et al.*, 2018a). These rapid responses have been shown to be highly  
37 species-specific and are expected to have major consequences on species interactions, species  
38 distributions, ecosystem functioning and forest carbon uptake (Cleland *et al.*, 2007; Chuine,  
39 2010; Richardson *et al.*, 2013). Therefore, accurately predicting plant species phenology at  
40 both large and local scales is of key importance for assessing the impact of global change on  
41 agro-ecosystems and the multiple services they provide, as well as species range shift and pop-  
42 ulations' local extinction.

43

44 Fu *et al.* (2015b) showed however that the linear trend towards earlier spring onset had been  
45 slowing down significantly during the last two decades. One of the hypothesis put forward by  
46 the authors to explain this slowdown is the warming of winters. And indeed, recently, Asse  
47 *et al.* (2018) documented the negative effect of the warming of winter on the leaf unfolding and

48 flowering date of several tree species. Air temperature is the major environmental factor regu-  
49 lating the dates of budburst and flowering of plants (Rathcke & Lacey, 1985; Polgar & Primack,  
50 2011). In perennial species, temperature has an antagonistic effect on bud development depend-  
51 ing on the season: low temperature (called chilling) are required to release the endodormancy  
52 of buds during winter, which is characterized by the inability of bud cells to growth despite  
53 optimal growing conditions, while higher temperature (called forcing) are required to promote  
54 bud cell elongation in spring. Recently, the effect of long photoperiod in compensating the lack  
55 of chilling temperature has also been reported for some tree species (Laube *et al.*, 2014; Way &  
56 Montgomery, 2015; Zohner *et al.*, 2016).

57

58 Our understanding of the environmental cues affecting species-specific bud break dates has  
59 been increasing thanks to the compilation of large phenological datasets (Menzel *et al.*, 2006; Fu  
60 *et al.*, 2015b), and to experimental work in controlled conditions using growth chambers (e.g.  
61 Caffarra & Donnelly 2011; Zohner *et al.* 2016). This empirical knowledge has been essential  
62 for the development and calibration of process-based phenology models (Chuine & Regniere,  
63 2017), that are used to predict spring phenology over large spatial and temporal scales (e.g.  
64 Chuine *et al.* 2016; Gauzere *et al.* 2017). While the relative contribution of environmental cues  
65 in driving spring phenological responses in current and future climatic conditions is still debated  
66 for most species (Chuine & Regniere, 2017; Laube *et al.*, 2014; Fu *et al.*, 2015a,b), the recent  
67 declining of the response of spring onset to global warming suggests that the relative influence  
68 of environmental cues driving the endodormancy phase varies with climatic conditions. Since  
69 climate change is likely to generate non-equilibrium conditions, the relative influence of the en-  
70 vironmental cues might also not remain constant over time. Overall, a strong expectation is that  
71 the environmental cues releasing endodormancy should have an increasing influence in warmer

72 environmental conditions. Yet, comprehensive analysis of the behavior of phenology models in  
73 different climates are still lacking, while pioneer modeling studies in crops have shown that it is  
74 expected to change depending on ecological conditions (*e.g.* Yin *et al.* 2005; Zhang *et al.* 2014).

75

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

88

89 For forest tree species, most studies in phenology modeling have focused on the analysis  
90 of extrinsic sources of variation, *e.g.* investigating the uncertainty of climatic inputs on sim-  
91 ulations (Morin & Chuine, 2005; Migliavacca *et al.*, 2012). Ecological studies interested in  
92 intrinsic sources of variation most often evaluate the effect of the variation of single parameters  
93 on the model outputs, other parameters remaining fixed at a given default value (*e.g.* Lange  
94 *et al.* 2016). The major disadvantage of this approach is to neglect possible interactions among  
95 parameters and to be unreliable in presence of non-linear relationships between the parameters

96 and the model predictions (Coutts & Yokomizo, 2014). At the opposite, sensitivity analyses  
97 varying all parameters simultaneously allow to account for parameter interactions and non-  
98 linear relationships and providing robust sensitivity measures for complex simulation models.  
99 While phenology model complexity is increasing with our understanding of the physiological  
100 responses involved in bud development, these interaction effects and non-linear relationships  
101 can no more be overlooked. A first originality and aim of this study was thus to compare the  
102 behavior of phenology models with increasing complexity, and to disentangle the main and in-  
103 teraction effects of parameters on bud break date predictions.

104

105 The most commonly used phenology models are process-based, meaning that they describe  
106 known or suspected cause-effect relationships between physiological processes and some driv-  
107 ing factors in the organism's environment to predict the precise occurrence in time of various  
108 phenology events (see for review Chuine & Regniere 2017). The parameters of these models are  
109 either defined using parameter values measured in experimental controlled conditions, or statis-  
110 tically inferred from phenological and meteorological data using inverse modeling techniques.  
111 Since they describe causal relationships derived from experimental work, the sensitivity analy-  
112 sis of process-based models is supposed to reflect the sensitivity of the real processes (Saltelli  
113 *et al.*, 2000). Therefore, we can expect the sensitivity of phenology models to specific param-  
114 eters, *e.g.* driving the endodormancy phase, to change with varying climatic conditions. The  
115 impact of climate on observed and simulated bud break dates is expected to be complex, be-  
116 cause of the cumulative and antagonistic effects of temperature depending on the season on bud  
117 development (Chuine & Regniere, 2017). For this reason, we also aimed at testing the param-  
118 eter sensitivity of phenology models to climatic conditions. We thus analyzed model behavior  
119 under specific patterns of winter and spring temperatures, that produced either particularly early

120 or late bud break date. This study thus differ from that of Lange *et al.* (2016) which explored  
121 the behavior of phenology models in uniformly warmer or colder conditions all along the year.  
122 In the present study we used different observed climatically contrasted years with their specific  
123 weather patterns.

124

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

144 influence on the prediction of models with increasing model complexity.

145

## 146 **2 Material and methods**

### 147 **2.1 Process-based phenology models**

148 Process-based phenology models (see for review Chuine & Regniere 2017) are deeply grounded  
149 on experimental results which have accumulated over the last 50 years and describe how the de-  
150 velopment of buds, from dormancy induction in fall to bud break in spring, is determined by  
151 the individual or interactive effects of different environmental cues, notably temperature and  
152 photoperiod. Most of these models are based on the same framework (see Chuine & Regniere  
153 2017). Each development phase (*e.g.* endodormancy, ecodormancy) is described by a sub-  
154 model determining its reaction norms to various cues. Several response functions describing  
155 the reaction norms to various cues can combine by addition, multiplication, or composition.  
156 Development phases either are sequential (follow each other in time) or overlap (a phase can  
157 start before the end of the previous one).

158

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

167 of forcing units to reach bud break.

168

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

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

174 with  $T$  the daily average temperature.

175

176 **UNICHILL** – The UniChill model is a sequential two-phases model describing the cumula-  
177 tive effect of chilling temperatures on the development of buds during the endodormancy phase  
178 (first phase) and the cumulative effect of forcing temperatures during the ecodormancy phase.  
179 Like in the Uniforc model, bud break occurs when the accumulated rate of forcing,  $R_f$ , reaches  
180  $F^*$  (Eqn. 1).

181 The start of the ecodormancy phase corresponds to the end of the endodormancy phase,  $t_c$ ,  
182 which occurs when the accumulated rate of chilling  $R_c$  (Eqn. 8) has reached the critical state of  
183 chilling  $C^*$ :

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

184 **PGC** – The PGC model has been designed to explain bud break date of photosensitive  
185 species, which might represent about 30 % of the species (Zohner *et al.*, 2016). It has been

186 shown to be particular relevant to simulate the bud break date of beech (*Fagus sylvatica*) which  
 187 is one of the most photosensitive species for bud break (Gauzere *et al.*, 2017). This is a pho-  
 188 tothermal model that integrates the compensatory effect of photoperiod on insufficient chilling  
 189 accumulation through a growth competence function ( $GC$ ; Gauzere *et al.* 2017). The growth  
 190 competence function describes the ability of buds to respond to forcing temperatures. It modu-  
 191 lates the rate of forcing ( $R_f$ ) through a multiplicative function to define the actual daily forcing  
 192 units accumulated by the bud until bud break as:

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

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

194

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

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

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

197  $P_{50}$  is not constant and depends on the state of chilling ( $CS$ ): the greater the accumulated rate

198 of chilling, the shorter the mid-response photoperiod, i.e. buds become sensitive to shorter

199 photoperiod when they have accumulated chilling:

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

200 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

201 negative slope of the sigmoid function, and  $C_{50}$  is the mid-response parameter if the sigmoid

202 function, reflecting chilling requirements under short-day length.

203 Finally, chilling units accumulated as:

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

204

205

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

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

210 with  $d_T$  the positive slope and  $T_{50}$  the mid-response temperature of the sigmoid function.

211 We defined the rate of chilling,  $R_c$ , as a threshold function (Caffarra *et al.*, 2011b):

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

212 with  $T_d$ , the mean temperature of day  $d$  and  $T_b$ , the threshold temperature (also called base tem-  
213 perature) of the function.

214

215 As defined here, the UniForc model has 4 parameters ( $t_0$ ,  $d_T$ ,  $T_{50}$ ,  $F^*$ ), the UniChill model  
216 6 parameters ( $t_0$ ,  $T_b$ ,  $C^*$ ,  $d_T$ ,  $T_{50}$ ,  $F^*$ ), the PGC model 9 parameters ( $t_0$ ,  $T_b$ ,  $C_{50}$ ,  $P_r$ ,  $d_C$ ,  $d_P$ ,  $d_T$ ,  
217  $T_{50}$ ,  $F^*$ ; Table 1).

218

## 219 **2.2 Model calibration and validation**

220 In order to set up the sensitivity analysis design, we first calibrated and validated the studied  
221 phenology models for three emblematic tree species in European forests: common beech (*Fagus*  
222 *sylvatica* L.), sessile oak (*Quercus petraea* L.) and silver fir (*Abies alba* Mill.). These results  
223 were used to (i) define the natural parameter variation among tree species (Table 1) and (ii)  
224 identify contemporary climatic years that produced particularly early and late spring phenology  
225 (Appendix D). The three models were parametrized for the three different species using obser-  
226 vations of the bud break date in the Pyrenees and corresponding weather data from 2005 to 2012.  
227

228 The phenology of several populations located at different elevations following the Gave and  
229 Ossau valleys in the Pyrenees have been yearly monitored since 2005. The studied populations  
230 ranged from 131 to 1604 m (9 sites) for beech, from 131 to 1630 m (13 sites) for oak, and from  
231 840 to 1604 m (6 sites) for fir (for further details about these populations, see Vitasse *et al.*  
232 2009). Data used for this study consisted in the bud break date (BBCH 9) monitored from 2005  
233 to 2012 in these populations. Models were parametrized using daily weather data since 2004  
234 from Prosensor HOBO Pro (RH/Temp, Onset Computer Corporation, Bourne, MA 02532) that  
235 have been placed at the core of each monitored population (Vitasse *et al.*, 2009). Day length was  
236 calculated according to the latitude of the meteorological stations (see Caffarra *et al.* 2011a).  
237 Using these datasets, the three studied models were parametrized for each species following  
238 Gauzere *et al.* (2017). The models *RMSE* varied from 5.85 to 10 days, with mean *RMSE* of  
239 6.28 for beech, 6.92 for oak, 9.39 for fir (Appendix C).

240

### 241 2.3 Sensitivity analysis

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

255

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

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

263 with

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

264  $Y$  is the prediction and  $X_i$  the  $i^{\text{th}}$  parameter of the model. The notation  $(X \sim i)$  indicates the  
 265 set of all variables except  $X_i$ . The numerator represents the contribution of the main effect of  $X_i$   
 266 to the variation in the output, i.e. the effect of varying  $X_i$  alone, but averaged over variations in  
 267 other input parameters.  $S_i$  is standardized by the total variance to provide the fractional contri-  
 268 bution of each parameter  $i$ .

269

270 And total-effect index as:

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

271 with

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

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

275

## 276 2.4 Climatic data used for the sensitivity analysis

277 To perform the sensitivity analysis, we used the climate simulated at different elevations, over  
278 a gradient of 1000 m, for the period from 1956 to 2012, in order to explore a large range  
279 of climatic conditions. To study the response of the models to realistic climate at different  
280 elevations, we used measurements taken with local weather stations on three forest sites, at  
281 627 m, 1082 m and 1630 m a.s.l., along the Gave valley (Prosensor HOBO Pro; Vitasse *et al.*  
282 2009). As this weather dataset only covered the period from 2004 to 2012, we also used Météo  
283 France measurements at other stations located close to these sites, and data from the SAFRAN  
284 reanalysis on the points of the systematic grid located in the valley, to simulate the climate at  
285 the forest sites over a larger period (1959-2012). The temperature data recorded with the local  
286 HOBO sensors were linearly correlated to the climatic data derived by the SAFRAN model of  
287 Météo France (Quintana-Segui *et al.*, 2008) for the same period. Daily minimum and maximum  
288 temperature data from 1960 to 2012 were generated based on the long-term SAFRAN outputs  
289 using the following equation:

$$T(X) = \beta_t(X) + \alpha_t(X) \cdot T_{SAFRAN} \quad (13)$$

290 with  $X$  the targeted site,  $\beta_t$  and  $\alpha_t$  the intercept and the slope of the linear regression be-  
291 tween  $T_{SAFRAN}$  and  $T_{HOBO}$  for the period 2004-2012. The coefficients used for this equation are  
292 provided in Appendix A. Day length was calculated according to the latitude of the forest sites  
293 (see Caffarra *et al.* 2011a).

294

295 Over this large simulated period, we chose three climatically contrasted years, that corre-  
296 sponded to (1) a year with winter and spring mean temperatures close to their global mean over

297 the 1960-2012 period ("normal climatic year"; year 1966), (2) a year expected to produce early  
298 spring phenology, *i.e.* with cooler winter and warmer spring temperatures than normal ("early  
299 climatic year"; year 2011) and (3) a year expected to produce late spring phenology, *i.e.* with  
300 warmer winter and cooler spring temperatures than normal ("late climatic year"; year 1975;  
301 Table 2; Appendix B). We checked that the three years selected indeed generated early, average  
302 and late bud break dates using the adjusted models for different tree species (Appendix D). This  
303 range of climatic conditions allowed us to credibly investigate the impact of specific weather  
304 patterns in winter and spring on the behavior of the models.

305

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]
$d_T$	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	hours	[0.9; 1.5]	$\mathcal{U}$ [1; 6]
$d_C$	PGC	slope of photoperiod sensitivity response	hours/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/hours	[0.26; 11.9]	$\mathcal{B}_{\{\alpha=20;\beta=1.3\}}$ [10 <sup>-5</sup> ; 10]

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 E). DOY = day of the year; DU = developmental units; DR = developmental rate.

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

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).

## 306 **3 Results**

### 307 **3.1 Main trends in parameter sensitivity of phenology models**

308 For the three models, the mid-response temperature during the ecodormancy ( $T_{50}$ ) had the great-  
309 est influence on the predictions of the models in most of the climatic conditions explored, except  
310 in the cool winter-warm spring conditions producing early phenology (Figure 1, and see Ap-  
311 pendices F, G and H for detailed results). This strong influence is both due to the main effect of  
312  $T_{50}$  and its interaction with other parameters, and especially with  $d_T$ ,  $T_{50} \times d_T$  defining the shape  
313 of the forcing response during the ecodormancy phase. Under the conditions producing early  
314 phenology, the main parameters affecting the predicted bud break date were  $t_0$ ,  $T_{50}$  and  $F^*$  for  
315 UniForc, UniChill and PGC respectively (Figure 1a). Note that the influence of the parameters  
316 on the predictions of the models was significantly affected by their coefficient of variation (*i.e.*  
317 parameters that had the highest variation also had the highest influence; Figure 2). However,  
318 this effect only explained a small proportion of the total variation in the total-effect of the pa-  
319 rameters ( $R^2 = 0.29$ ).

320

### 321 **3.2 The sensitivity to model parameters varies with model complexity**

322 The sensitivity of model predictions to the variation in model parameters highly depended on  
323 the phases and processes modeled (Figure 1). Predictions of the ecodormancy model UniForc  
324 were more sensitive to the  $t_0$  parameter, *i.e.* the model starting date, than the predictions of  
325 the endo-ecodormancy models UniChill and PGC, particularly under the climatic conditions  
326 producing early phenology (Figure 1a and b). Predictions of the thermal model UniChill were  
327 more sensitive to the critical amount of chilling to release dormancy ( $C^*$  parameter) than the

328 predictions of the photothermal model PGC to the equivalent parameter ( $C_{50}$ ). Predictions of  
329 this latter photothermal model was more sensitive to the critical amount of forcing ( $F^*$ ) than  
330 that of the thermal models UniForc and UniChill. Finally, predictions of the UniChill model  
331 were more sensitive to the mid-response temperature during ecodormancy ( $T_{50}$ ) than that of the  
332 UniForc and PGC models, which presented similar sensitivity to this parameter (Figure 1).  
333 Depending on the model complexity, the uncertainty in the predictions will thus reply in the  
334 accurate calibration of different key parameters.

335

### 336 **3.3 The sensitivity to model parameters varies with climate**

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

347

348 The sensitivity of the predictions of the PGC model to both the critical amount of chilling  
349 ( $C_{50}$ ) and the parameter determining the sensitivity to photoperiod ( $d_p$ ) increased with warming  
350 temperature (Figure 3). But, in such conditions, the sensitivity of PGC model predictions to

351 the photoperiod related parameter was higher than that to chilling related parameters ( $C_{50}$  and  
352  $T_b$ ; Figure 3). Finally, the sensitivity of PGC model predictions to the starting date of endodor-  
353 mancy ( $t_0$ ) tended to increase with warming temperature conditions, while that of the Unichill  
354 model remained constant and low (Figure 3). This result may be explained by the differences  
355 in growth competence modeling between these two models. The growth competence function  
356 of the PGC model is not null in autumn but decreases with the decreasing day length, and in-  
357 duces endodormancy. If temperature conditions are particularly favorable, some forcing units  
358 can be accumulated before endodormancy is fully induced contrary to the Unichill model. This  
359 therefore gives an increasing importance to  $t_0$  in driving bud break dates in warmer temperature  
360 conditions.

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

363

### 364 **3.4 Main and interaction effects**

365 In the results above, we describe the influence of the parameters on the predictions of the mod-  
366 els based on their total effect, which include both main and second-order interaction effects.  
367 However, it is also interesting to decompose these effects to understand their relative contribu-  
368 tions to the variation of bud break dates. For most parameters, the total effects were mainly due  
369 to main (or first-order) effects, and in a lesser extend to interaction effects between parameters  
370 (or second-order effects; Figures 1). Second-order effects always explained less than 15 % of  
371 the predictions variation (while the largest first-order effect explained more than 50 % of the  
372 output variation ; Figure 4 and Appendix I). Interestingly, interaction effects did not modify the  
373 relative influence of the parameters on the predictions of the models (Figures 1). Nevertheless,

374 total interaction effects represented an important source of variation in the predicted bud break  
375 dates (Figure 4), in particular for the most complex models.

376

377 The total influence of interaction effects on model predictions also varied with the specific  
378 weather patterns in winter and spring. For UniForc, total interaction effects were found to be  
379 more important in the warm winter-cool spring conditions, producing late phenology, while for  
380 PGC, these effects were more important in the cool winter-warm spring conditions, producing  
381 early phenology (Figure 4a and c). The interaction between the parameters  $T_{50}$  and  $d_T$  had the  
382 largest effect on the predicted bud break date, notably in the coldest temperature conditions  
383 ( $d_T \times T_{50}$ ; Appendices I). These two parameters define the shape of the response to temper-  
384 ature during ecodormancy in the three models. For the PGC model in the warmest climatic  
385 conditions, the interaction between the endodormancy starting date ( $t_0$ ) and the photoperiod  
386 sensitivity ( $d_P$ ) also had an impact on the predicted bud break date ( $t_0 \times d_P$ ; Appendix I).  
387 The influence of interaction effects thus tended to increase with model complexity, but also  
388 varied with specific weather patterns in winter and spring.

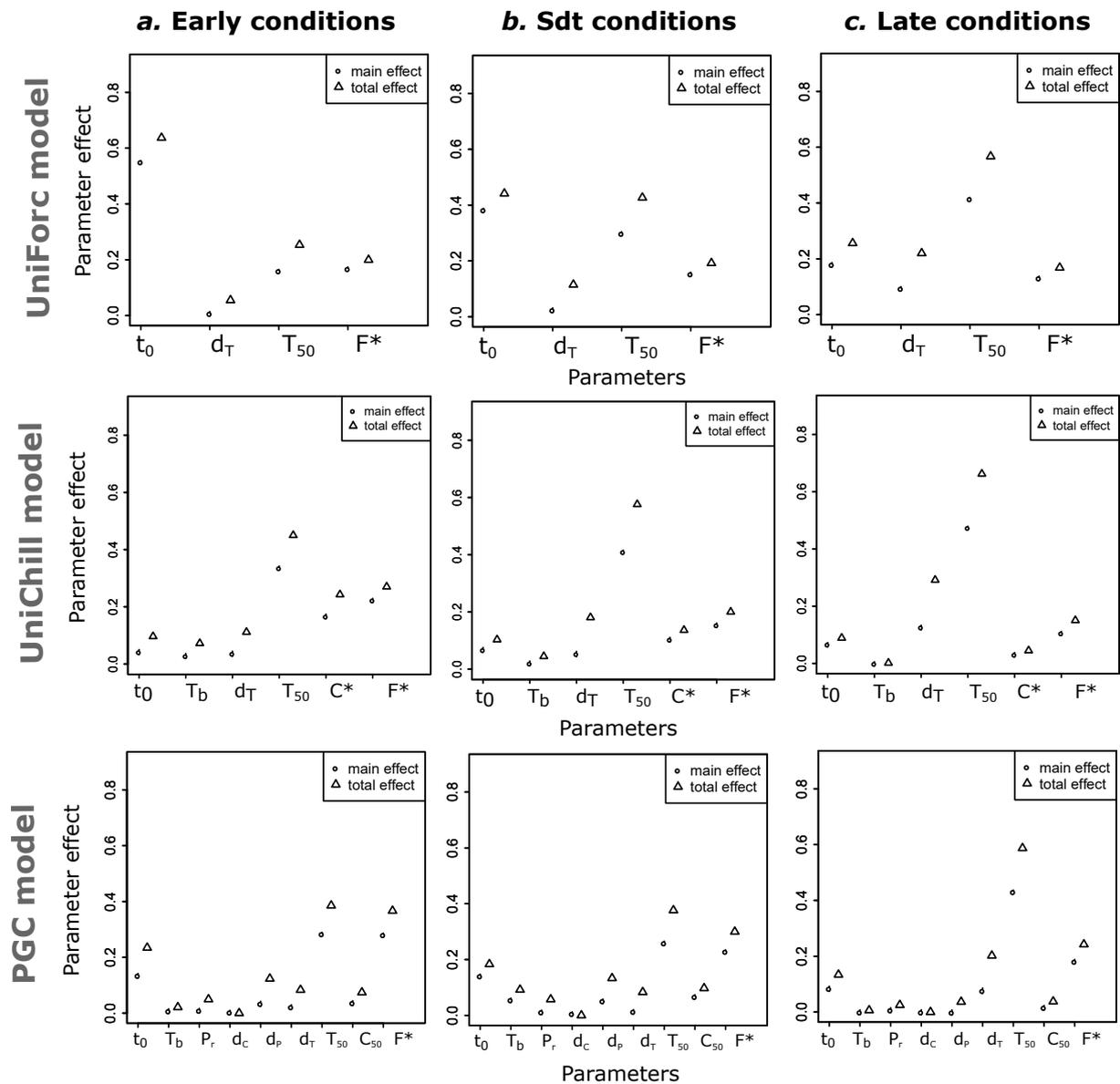


Figure 1: Main and total effects of the parameters on the predictions of the three studied models in the most contrasted climatic conditions. The main effect (or first-order effect) quantifies the individual effect of a parameter, *i.e.* without interactions. The total effect represents the first- and 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 H.

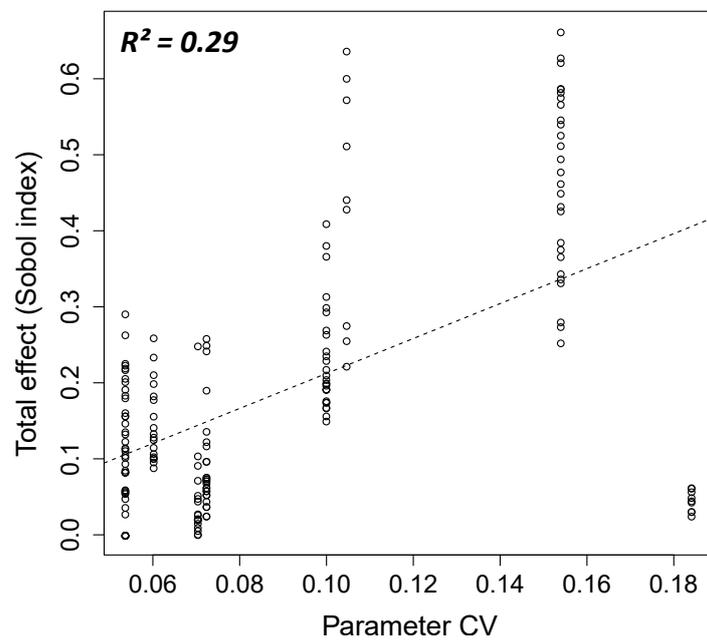


Figure 2: Variation in the total-effect of parameters on the predictions of all models according to their coefficients of variation ( $CV$ ). The coefficient of variation of each parameter was estimated from its sampling distribution. The  $R$ -squared was estimated using a linear model. The parameters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

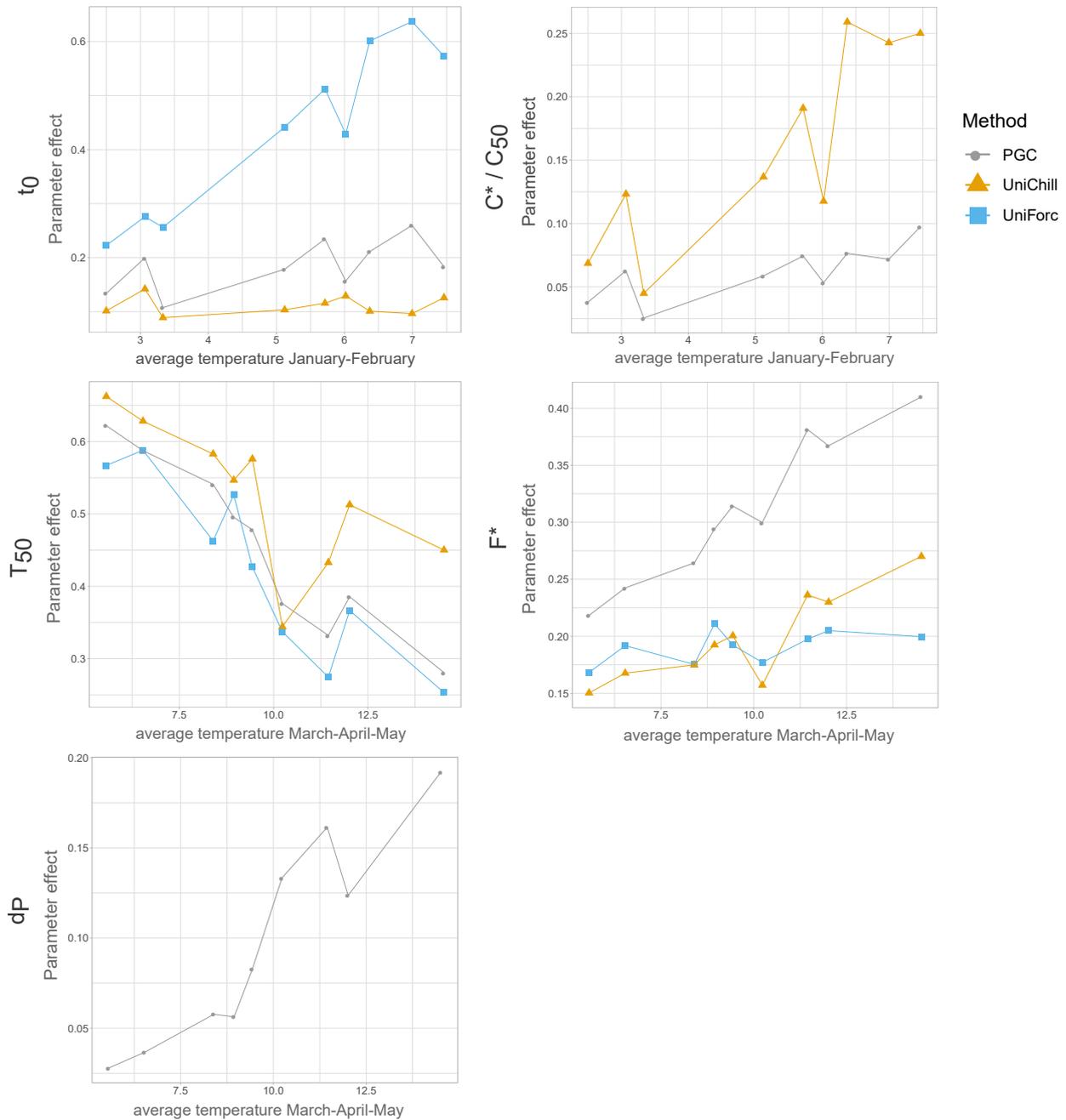


Figure 3: Variation in the total effect of the most biologically relevant parameters on the predictions of the three studied models according to climatic variables (see also Appendix G). The total effect quantifies the proportion of variance in the model's prediction explained by the variation of a given 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.

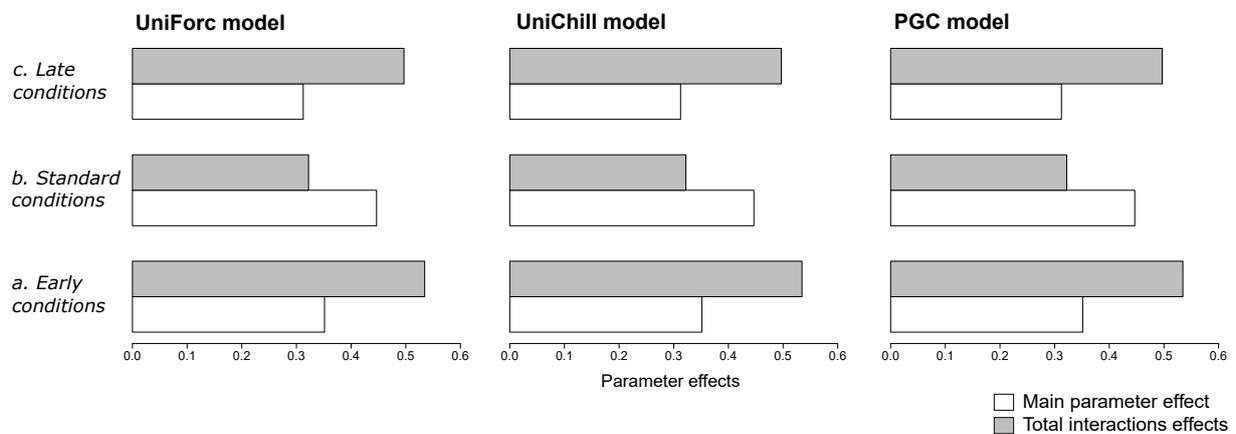


Figure 4: Proportion of the variation in model predictions explained by the main individual parameter effect and the total interaction effect for each model under the three most contrasted climatic conditions. The main parameter individual effects is the proportion of variance in the predictions explained by the most influential parameter ( $T_{50}$  in most cases). The total interaction effects is 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.

## 389 4 Discussion

### 390 4.1 Bud break date predictions mainly depend on the forcing response under current 391 climatic conditions

392 The sensitivity analysis of the studied process-based models showed that the mid-response tem-  
393 perature of the ecodormancy phase (called here  $T_{50}$ ) plays a critical role in the prediction of bud  
394 break date under current climatic conditions. This result applies whether models account or not  
395 for an endodormancy phase or a photoperiodic control of bud development. It therefore suggests  
396 that the response to forcing temperature during the ecodormancy (defined by both  $T_{50}$  and  $d_T$  in  
397 the studied phenological models) is a major physiological response driving the variation of bud  
398 break dates in temperate plant species in historical and current climatic conditions. This finding  
399 is consistent with previous correlative modeling studies showing that bud break date variation  
400 was mainly driven by the mean temperature of the two preceding months, which roughly corre-  
401 sponds to the ecodormancy phase (*e.g.* Menzel *et al.* 2006). It is also consistent with previous  
402 process-based modeling studies showing that models simulating only the ecodormancy phase  
403 explained as much variance in bud break dates as models simulating both the endo- and ecodor-  
404 mancy phases (Linkosalo *et al.*, 2006; Gauzere *et al.*, 2017). The similar performance of the  
405 two types of model suggested either that the fulfillment of chilling requirements had not been  
406 a limiting factor so far, or that the endodormancy phase is not accurately modeled (Linkosalo  
407 *et al.*, 2006; Chuine *et al.*, 2016). Our results support the first hypothesis, *i.e.* winter chilling  
408 temperature have played a minor role in bud break variations so far, which also explains why  
409 the response of plant species to climate warming has so far resulted in an advancement of the  
410 bud break dates (Menzel *et al.*, 2006). A methodological consequence of this is that phenolog-  
411 ical records in natural populations may not allow estimating accurately endodormancy model

412 parameters (Chuine *et al.*, 2016).

413

## 414 **4.2 Bud break date predictions are increasingly dependent on chilling temperatures and** 415 **photoperiod as climate warms**

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

431

432 The sensitivity analysis of the photothermal endo-ecodormancy model PGC showed that the  
433 influence of the photoperiodic response (through the  $d_P$  parameter) on the prediction of the bud  
434 break date increased in warmer environmental conditions. A growing number of studies suggest

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

444

### 445 **4.3 Originality and limits of the study**

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

453

454 To our knowledge, this study is the first to have compared the behavior of different phenol-  
455 ogy models, with increasing complexity, and to perform this analysis under different weather  
456 patterns in winter and spring. The results found here are in line with a recent sensitivity anal-  
457 ysis of species-specific phenology models, which found an increasing importance of chilling

458 requirements and photoperiod in warm climatic conditions for temperate tree species (Lange  
459 *et al.*, 2016). The consistency of our results with the sensitivity analysis of other phenology  
460 models strengthens the scope of our study, and thus further stress the importance of investigat-  
461 ing the behavior of phenology models in contrasted climatic conditions in order to fully embrace  
462 their robustness.

463

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

473

474 Due to the high computational requirement of sensitivity analyses, most studies usually ne-  
475 glect, partially or completely, interaction effects between model parameters as a source of output  
476 variation (*e.g.* Lange *et al.* 2016). However, the complexity of process-based phenology models  
477 tends to increase as we gain better knowledge about the physiological processes involved in bud  
478 development. With increasing model complexity and realism, we can expect interaction effects  
479 to have non-negligible influence on the prediction of the models, and thus local sensitivity anal-  
480 ysis to partially reveal the effect of parameters on output variance. Our results also suggest that  
481 model complexity would result in higher uncertainty in bud break dates because of interaction

482 effects. Moreover, increasing model complexity would generate higher uncertainty in model  
483 outputs because of parameter compensation during the statistical adjustment, notably if models  
484 are used to perform predictions outside of the range of the climatic conditions used to adjust  
485 them (Gauzere *et al.*, 2017).

486

487 Here, we showed that sensitivity analysis of process-based phenology models are relevant  
488 to identify key parameters and processes that have the largest effect on phenology (Migliavacca  
489 *et al.*, 2012; Lange *et al.*, 2016). However, the choice of the parameter variation range likely  
490 affects the results of such analyses. Since for most plant species, the range limits or shape of the  
491 distributions of the physiological parameters in natural populations are unknown, such sensitiv-  
492 ity analyses rely on assumptions that cannot be tested. Here, we might have overestimated the  
493 real contribution of  $T_{50}$  and  $F^*$  to the variation of the bud break date due to uneven variances in  
494 parameter sampling distributions. This effect of parameter variation on the outcome of sensitiv-  
495 ity analyses should be more acknowledged. To improve the scope and relevance of sensitivity  
496 analyses, more attention should be given to the characterization of the natural variation of the  
497 physiological parameters described in process-based models (*e.g.* Burghardt *et al.* 2015).

498

#### 499 **4.4 Implications for the adaptive potential of phenological traits**

500 While the sensitivity analysis of phenology models has direct implications for ecological and  
501 climate change studies, we wanted to highlight also here their usefulness for evolutionary stud-  
502 ies. The bud break date is among the most genetically differentiated trait across species dis-  
503 tribution ranges (De Kort *et al.*, 2013), suggesting that it is strongly involved in the process of  
504 local genetic adaptation. Evolutionary response of the bud break date is expected to depend on

505 which parameters present genetic variation and how this variation impacts the bud break date,  
506 *i.e.* the expressed trait variation. Sensitivity analysis outputs can be used to address this second  
507 issue. For example, our results show that the mid-response temperature of the ecodormancy  
508 phase ( $T_{50}$ ) has the highest impact on the variation of the bud break date in most conditions.  
509 We thus suggest that future experimental research consider measuring the genetic variation of  
510 this key physiological trait in natural populations and crops to evaluate their adaptive potential.  
511 This can be done by monitoring bud break of several genotypes either in varying controlled  
512 conditions (*e.g.* Caffarra *et al.* 2011b), or by monitoring growth transcriptor factors in natura  
513 or in the field using new transcriptomic technics (*e.g.* Nagano *et al.* 2012), or even better by  
514 combining both approaches (*e.g.* Satake *et al.* 2013). Given the increasing importance of the  
515 response to chilling temperatures during the endodormancy phase to determine the bud break  
516 date in warming conditions, future experimental research might additionally consider measur-  
517 ing the genetic variation in chilling requirement and reaction norms to chilling temperature,  
518 especially in species requiring large amount of chilling. Finally, future experimental research  
519 should consider measuring the genetic variation in the reaction norm to photoperiod in most  
520 sensitive species, and notably beech (Goyne *et al.* 1989 for example in crops).

521

## 522 **5 Conclusions**

523 The identification of the physiological responses underlying the bud break date variation in cur-  
524 rent environmental conditions is an important on-going experimental research field (Fu *et al.*,  
525 2015a,b; Vitasse *et al.*, 2018b). Assuming that process-based phenology models reflect real  
526 physiological responses and processes, the analysis of their behavior under contrasted climatic  
527 conditions can provide valuable information about this issue. Our results highlighted the ma-

528 jor influence of the response to forcing temperature on the prediction of the bud break date,  
529 but also an increasing importance of the responses to chilling temperature and photoperiod in  
530 warming environmental conditions. Changes in the sensitivity of the prediction of phenology  
531 models to their parameters with climatic conditions highlights that we need to better take into  
532 account the temporal and spatial variation of environmental conditions when analyzing pheno-  
533 logical changes (Vitasse *et al.*, 2018b). More generally, we acknowledge here that the sensitivity  
534 analysis of process-based models is a useful tool to understand the relative contributions of envi-  
535 ronmental cues in driving phenotypic traits variation and their evolutionary potential (Donohue  
536 *et al.*, 2015; Burghardt *et al.*, 2015; Lange *et al.*, 2016).

537

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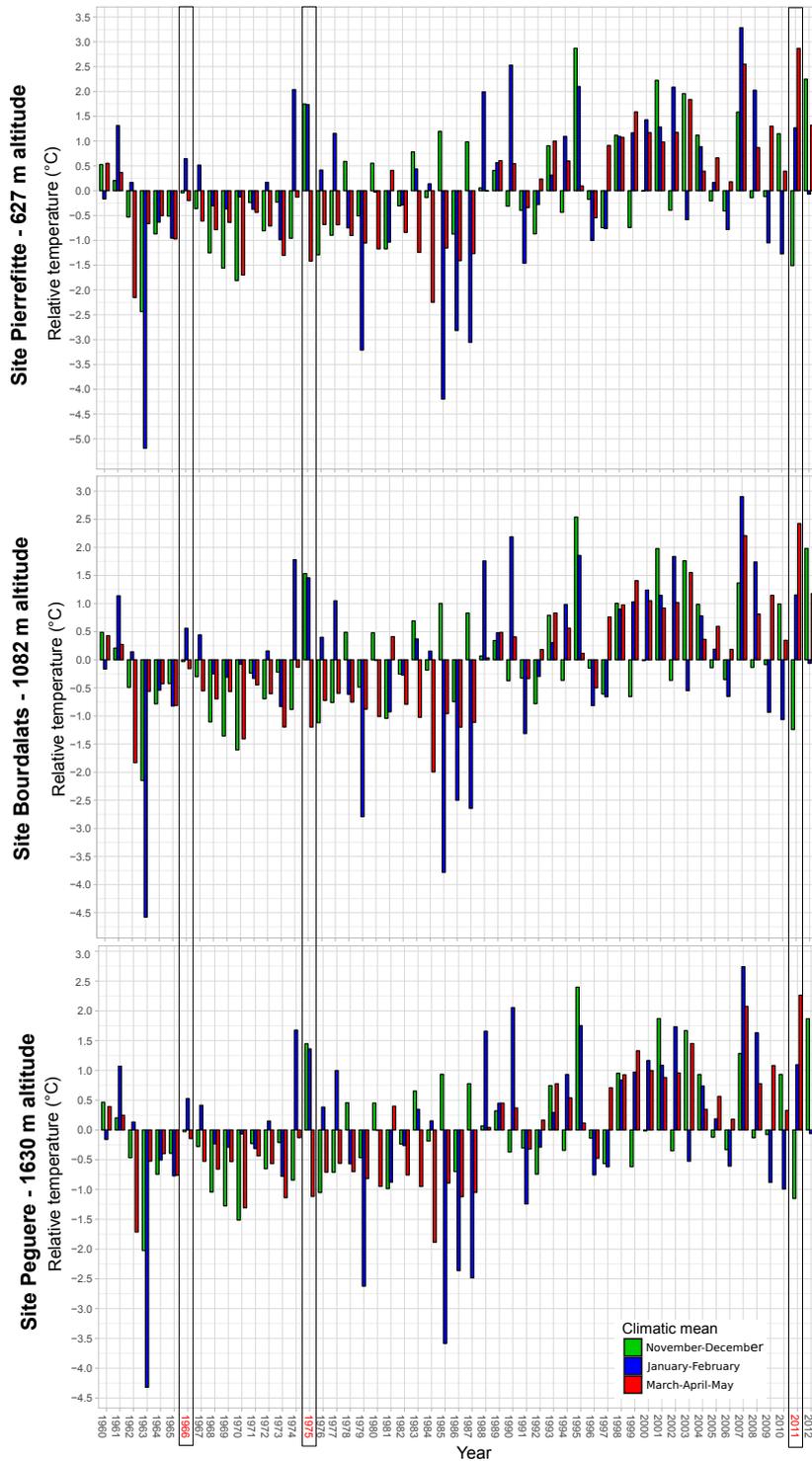
688 **Appendix A**

689 Coefficients of the equation used to reconstruct maximum and minimum temperatures at the  
690 three study sites.  $\beta_T$  and  $\alpha_T$  are the intercept and the slope of the linear relationship linking the  
691 recorded HOBO temperatures at the study site and the SAFRAN climatic data (from 2006 to  
692 2012).  
693

Elevation (m)	$\beta_{Tmax}$	$\alpha_{Tmax}$	$\beta_{Tmin}$	$\alpha_{Tmin}$
627	0.96	1.17	1.07	0.96
1082	3.98	0.93	1.74	0.99
1630	2.95	1.04	0.81	0.97

694 **Appendix B**

695 Yearly mean temperatures for the months (1) November-December ("meanND"), (2) January-February  
 696 ("meanJF") and (3) March-April-May ("meanMAM") relatively to their historic mean (period 1960-  
 697 2012) for the three studied sites at low (627 m), intermediate (1082 m) and high (1630 m) elevations  
 698 in the Pyrenees valley. Year 1966 was considered as an "average" climatic year, year 1975 as a "late"  
 climatic year and year 2011 as an "early" climatic year for the global sensitivity analysis.





699 **Appendix C**

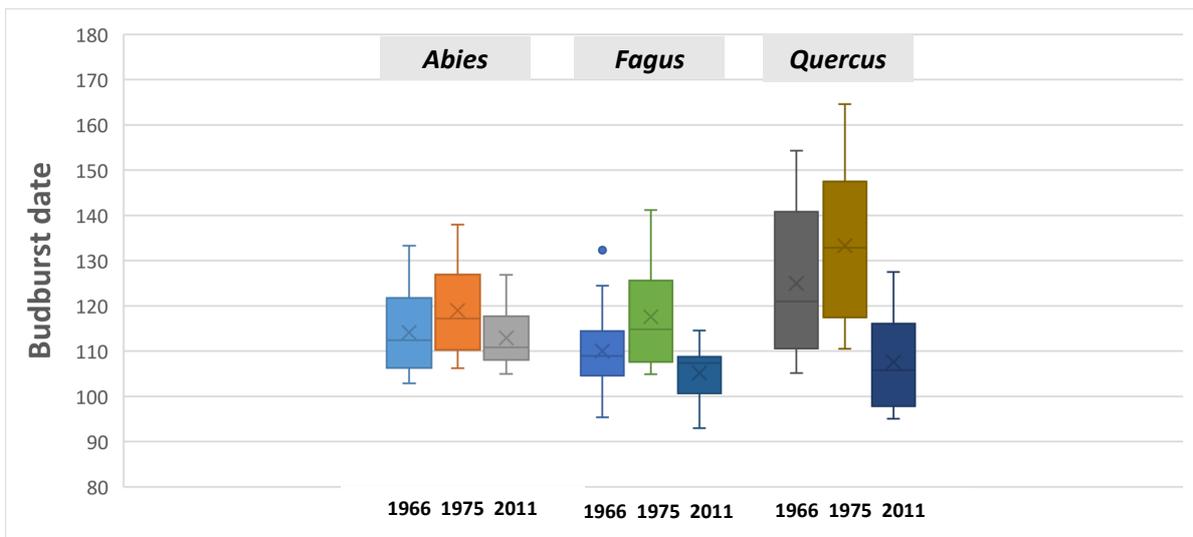
700 RMSE (days) and AIC of the three models for the three species calculated with all available bud break  
 701 date data for each species. Number of data for each species were 142 for *Fagus sylvatica*, 145 for *Quer-*  
 702 *cus petraea* and 95 for *Abies alba*.

703

	<i>Fagus</i>		<i>Quercus</i>		<i>Abies</i>	
	RMSE	AIC	RMSE	AIC	RMSE	AIC
UniForc	6.29	530.4	7.03	690.4	10.00	445.5
UniChill	6.72	553.0	6.98	692.2	9.07	430.9
PGC	5.85	519.6	6.76	686.8	9.45	444.8

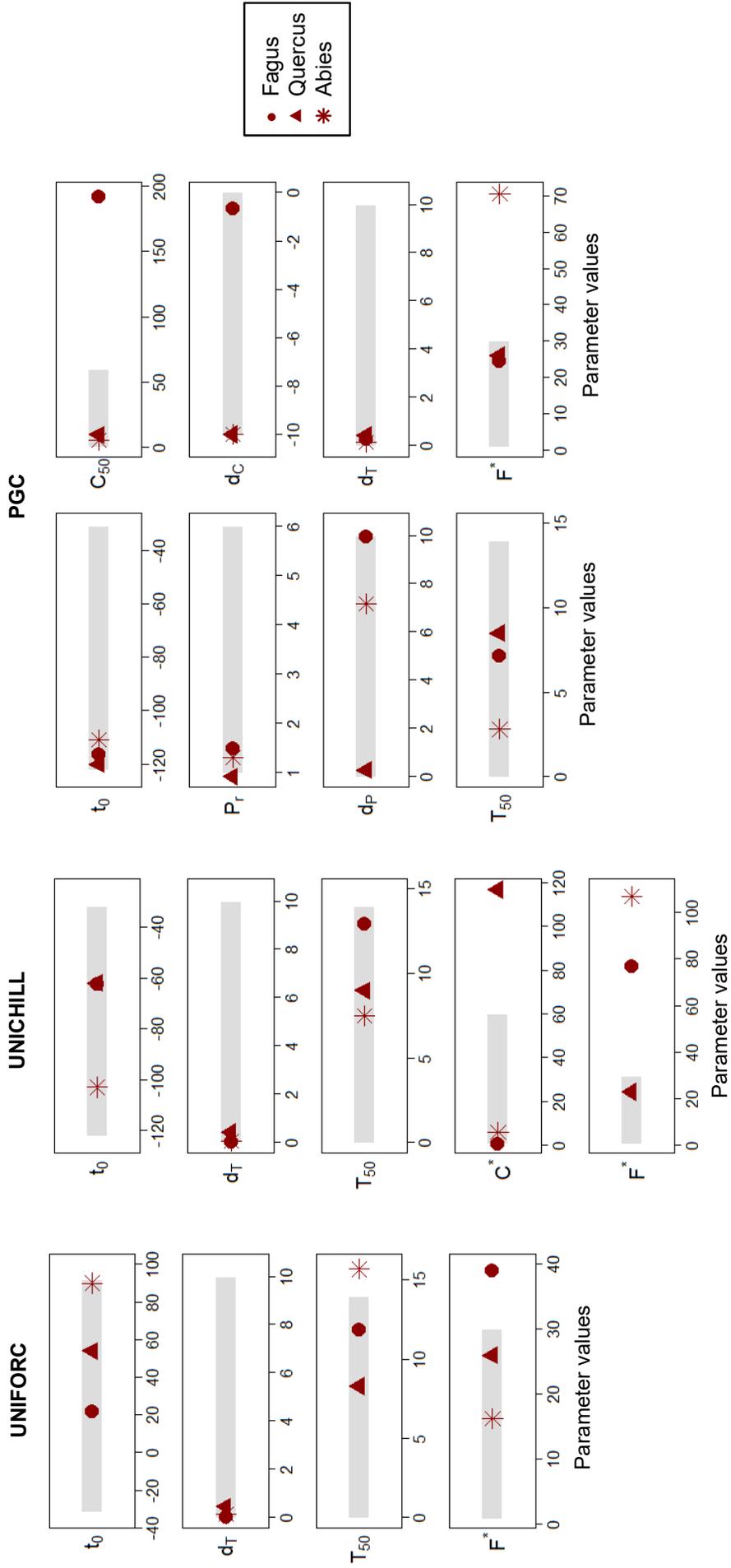
704 **Appendix D**

705 Variation in the bud break dates predicted by the best model calibrated and validated for *F. sylvatica*  
706 (*PGC*), *Q. petraea* (*UniChill*) and *A. alba* (*UniChill*). The best model for each species was chosen based  
707 on its statistical performance (RMSE) and the biological realism of its adjusted parameters (for more  
708 details see *Gauzere et al. 2017*). These projections were made using the climate corresponding to the 3  
709 focus years and along the studied elevation gradient of the Pyrenees. As expected, the climatic conditions  
710 in year 1975 generated on average late bud break dates, the conditions in year 2011 generated on average  
711 early bud break dates, and the conditions in year 1966 generated intermediate bud break dates.



## 712 Appendix E

713 Sampling distributions of the parameters of the three models used to perform the global sensitivity analy-  
714 sis. For all parameters, except slope parameters, values were drawn in uniform distribution  $\mathcal{U}$ . For slope  
715 parameters  $d$ , values were drawn in beta distribution  $\mathcal{B}_{\{\alpha=20;\beta=1.3\}}$ . On the graphic, the grey rectangles  
716 represent the range of parameter values explored by our simulations for the three studied models. The  
717 red symbols represent the parameters adjusted for *Fagus sylvatica* (dots), *Quercus petraea* (triangles)  
718 and *Abies alba* (stars) using bud break date observations in the Pyrenees. Most of the parameters values  
719 adjusted for the species were found in the range of variation explored by the sensitivity analysis. A no-  
720 table exception is for the critical amount of forcing and chilling rates,  $F^*$  and  $C^*$  (or  $C_{50}$ ) respectively.  
721 For  $F^*$ , many experiments in controlled environmental conditions have shown that the amount of days  
722 to reach bud break under optimal conditions was rarely over 30 days. But, in most cases, the adjust-  
723 ment of  $F^*$  is not constrained, which can lead to the adjustment of a parameter value with low biological  
724 realism. For  $C^*$  (and  $C_{50}$ ), the range of values explored by our simulations is lower than the adjusted  
725 range of  $C^*$  values because of methodological constraints. Indeed, sampling  $C^*$  values over 60 generated  
726 non-positioned bud break dates in warm conditions. So, we had to restrain the range of parameter values  
727 explored by the sensitivity analysis.



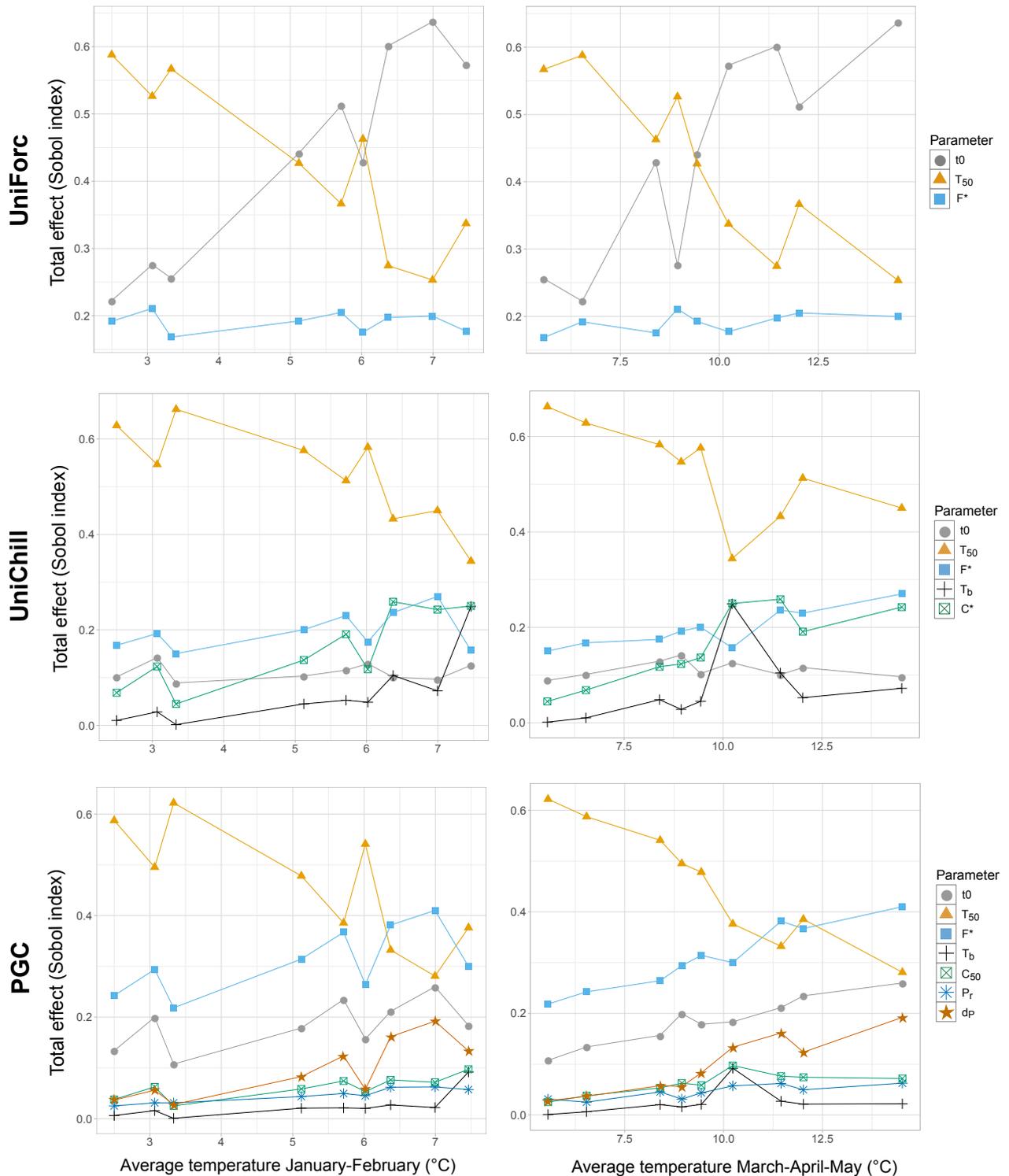
728 **Appendix F**

729 Total effect (eq. 12) of each parameter on the prediction of three studied models for the nine contrasted  
 730 climatic conditions. This coefficient reflects the contribution of each parameter to the prediction of the  
 731 bud break date, including all variances caused by its interactions with other parameters.  
 732

Elevation	Year	Method	e	t0	Tb	Pr	dP	Fcrit	Ccrit
627	1966	UniForc	0.275	0.601	-	-	-	0.197	-
627	1966	UniChill	0.433	0.101	0.104	-	-	0.236	0.259
627	1966	PGC	0.332	0.211	0.027	0.062	0.161	0.381	0.076
627	1975	UniForc	0.337	0.573	-	-	-	0.177	-
627	1975	UniChill	0.344	0.126	0.249	-	-	0.157	0.250
627	1975	PGC	0.376	0.183	0.092	0.057	0.133	0.300	0.097
627	2011	UniForc	0.253	0.637	-	-	-	0.200	-
627	2011	UniChill	0.450	0.096	0.072	-	-	0.270	0.243
627	2011	PGC	0.281	0.260	0.022	0.063	0.192	0.410	0.072
1082	1966	UniForc	0.427	0.442	-	-	-	0.192	-
1082	1966	UniChill	0.576	0.103	0.045	-	-	0.200	0.137
1082	1966	PGC	0.478	0.179	0.021	0.044	0.083	0.314	0.059
1082	1975	UniForc	0.463	0.429	-	-	-	0.175	-
1082	1975	UniChill	0.583	0.129	0.049	-	-	0.175	0.118
1082	1975	PGC	0.541	0.157	0.020	0.045	0.058	0.264	0.053
1082	2011	UniForc	0.367	0.512	-	-	-	0.205	-
1082	2011	UniChill	0.513	0.116	0.053	-	-	0.230	0.191
1082	2011	PGC	0.386	0.235	0.021	0.050	0.124	0.367	0.074
1630	1966	UniForc	0.588	0.222	-	-	-	0.192	-
1630	1966	UniChill	0.628	0.101	0.010	-	-	0.168	0.069
1630	1966	PGC	0.587	0.134	0.006	0.025	0.037	0.242	0.038
1630	1975	UniForc	0.567	0.256	-	-	-	0.168	-
1630	1975	UniChill	0.662	0.089	0.002	-	-	0.150	0.045
1630	1975	PGC	0.622	0.108	0.001	0.031	0.028	0.218	0.025
1630	2011	UniForc	0.526	0.276	-	-	-	0.211	-
1630	2011	UniChill	0.547	0.142	0.028	-	-	0.192	0.123
1630	2011	PGC	0.495	0.200	0.016	0.031	0.056	0.294	0.063

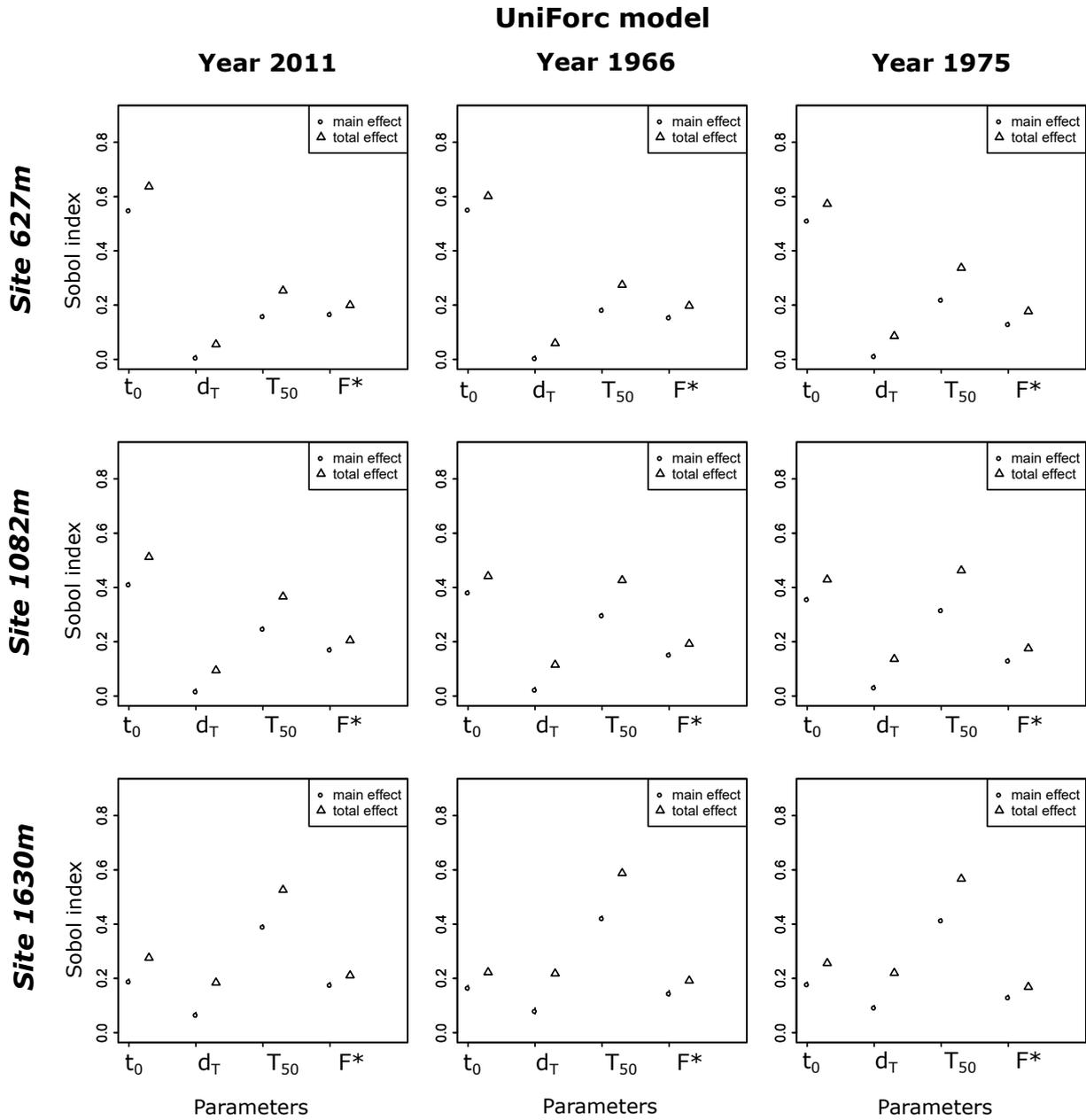
733 **Appendix G**

734 Variation in the total effect (i.e. first and second-order effects) of all parameters on the prediction of  
 735 the three studied models according to the climatic conditions. Only the parameter's total effect on the  
 736 prediction is represented. The climate was here described by the average temperature in January and  
 737 February (known to be important to release dormancy), and average temperature in March, April and  
 738 May (important during the ecodormancy). The climatic gradient is thus described by the 9 contrasted  
 739 climates we used to perform the sensitivity analyses.

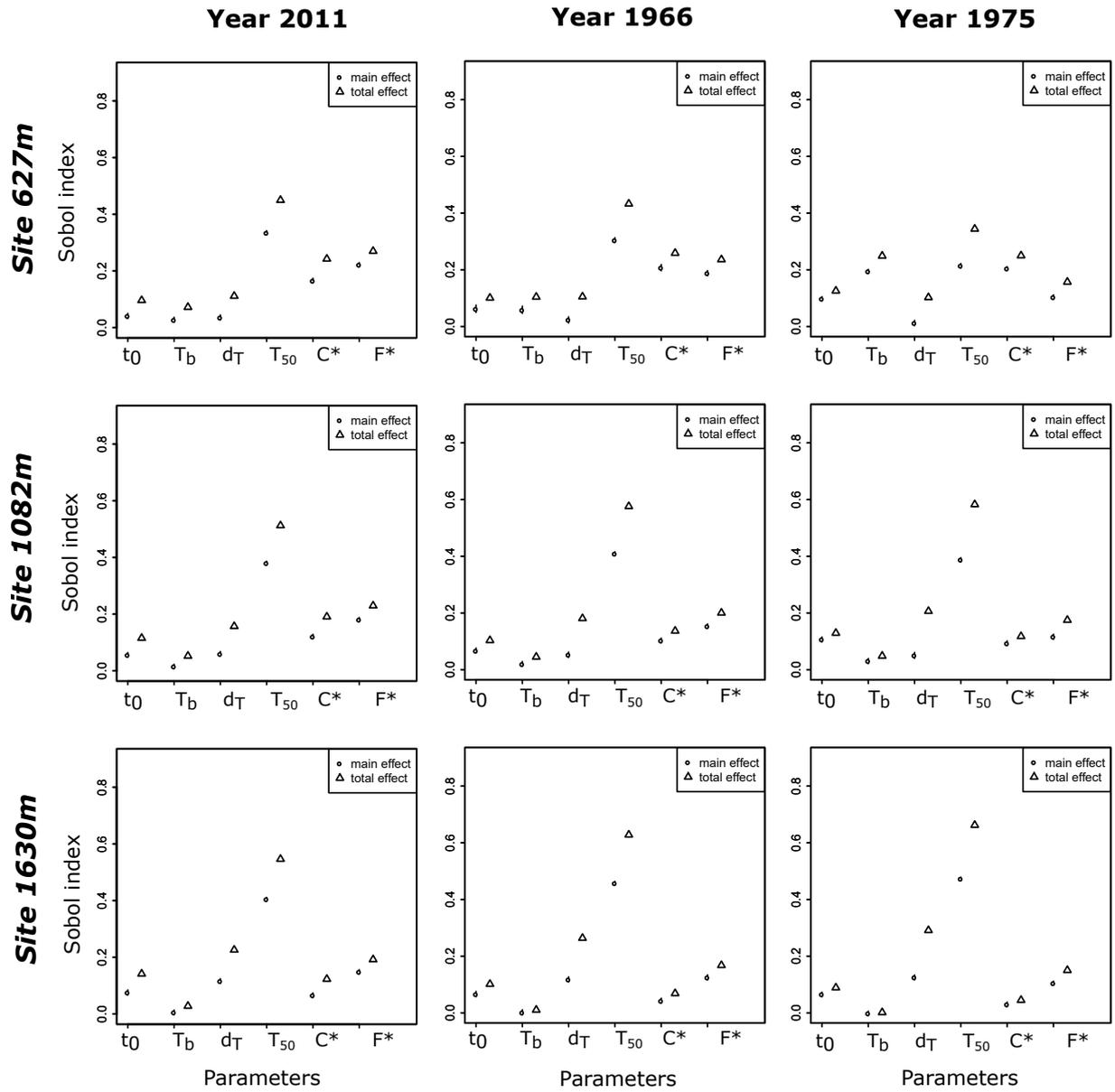


740 **Appendix H**

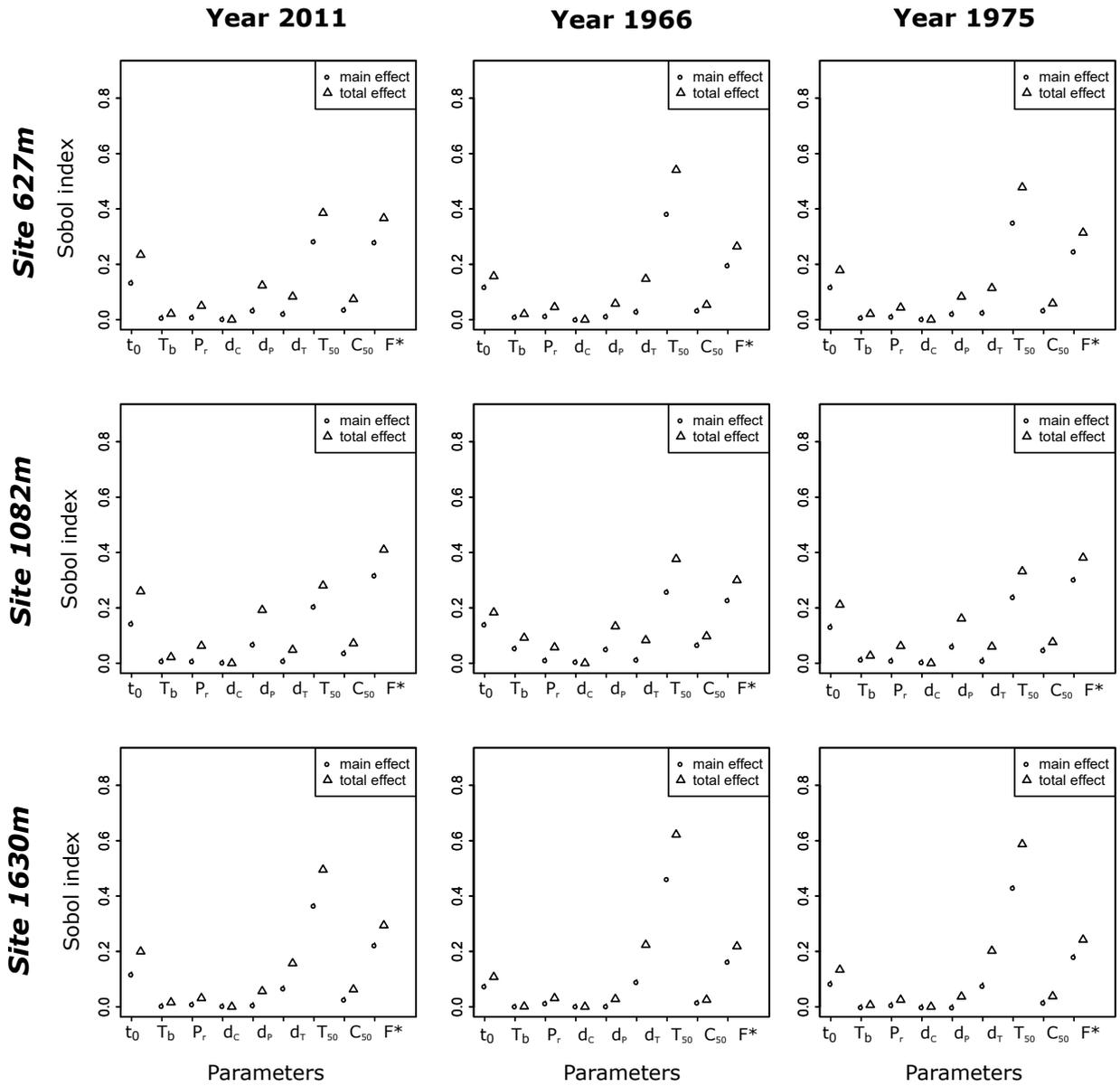
741 Main and total effects of the parameters on the prediction of the models for the nine contrasted climatic  
 742 conditions. From left to right and top to down are ranked the earlier to the later climatic years, with 2011  
 743 the early climatic year, 1966 the average climatic year and 1975 the late climatic year.



## UniChill model

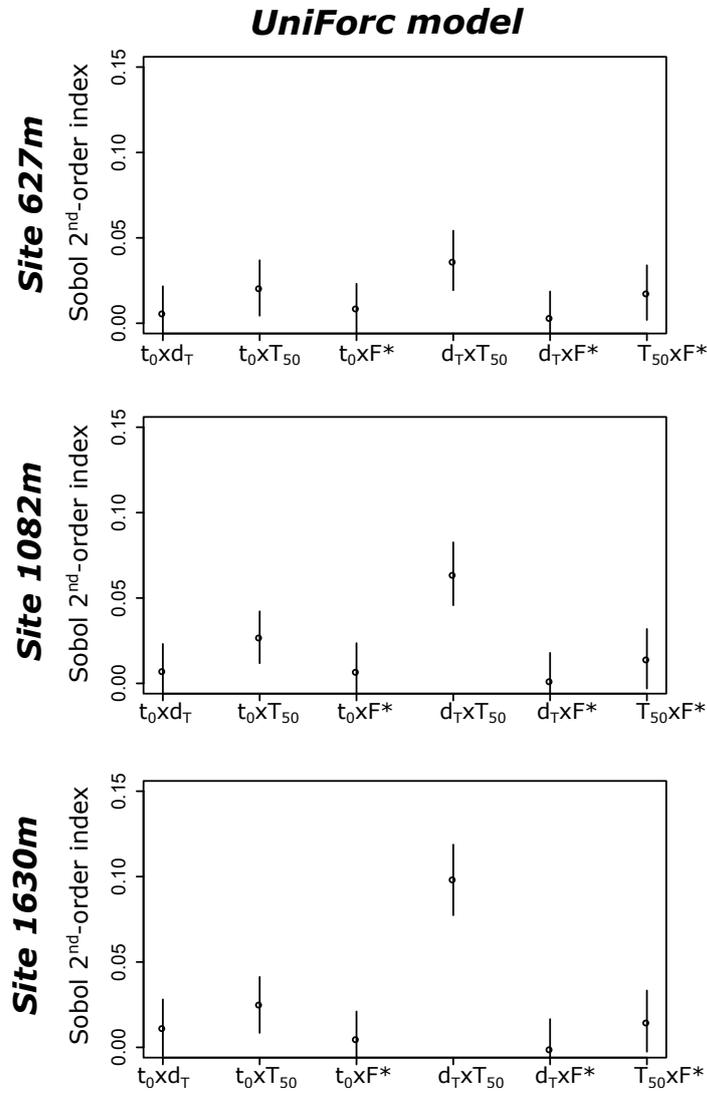


## PGC model

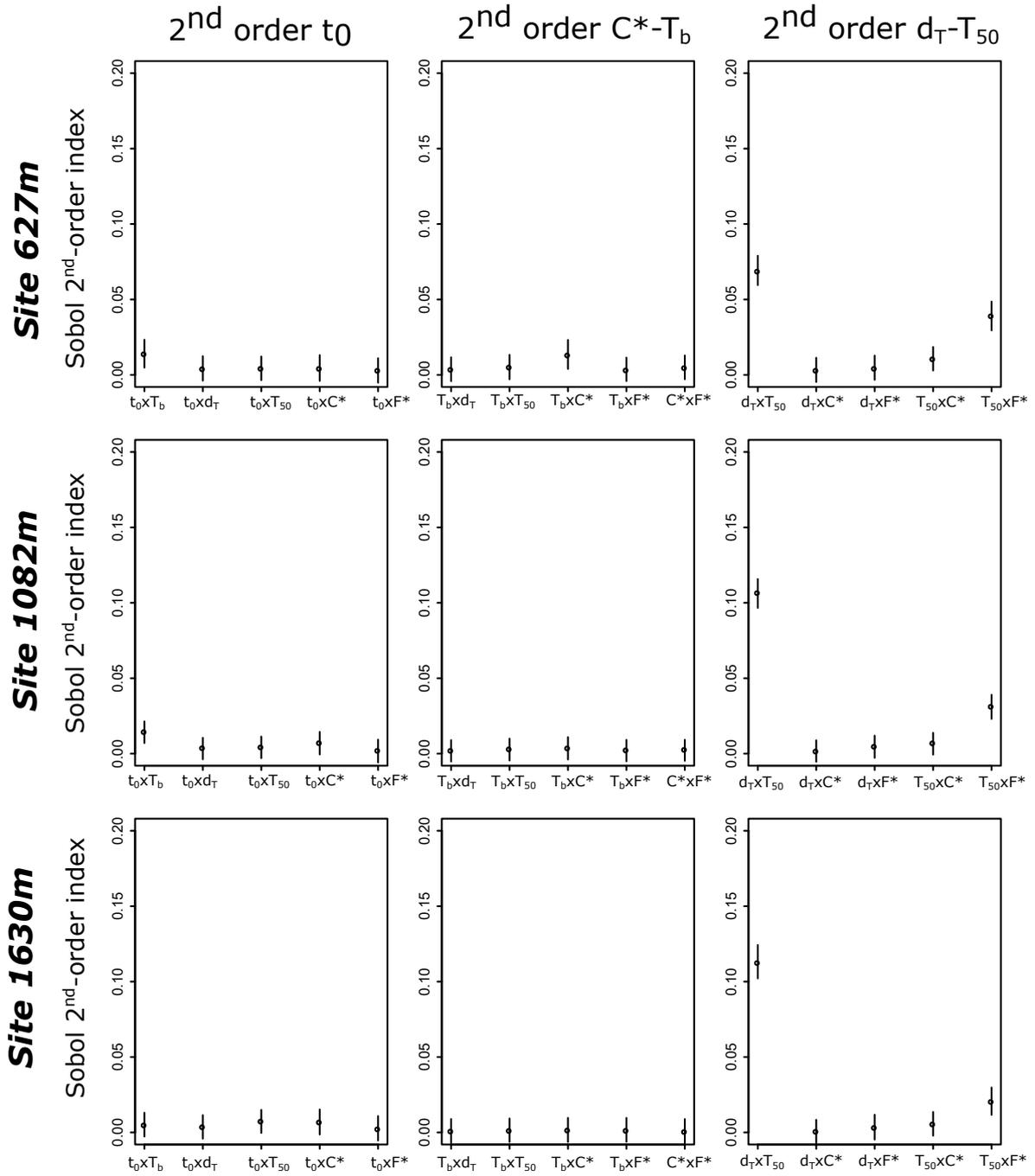


744 **Appendix I**

745 Second-order effects on the prediction of the models for the three elevation sites the average climatic  
746 year 1966. These second-order effects quantify the impact of pairwise interactions between parameters  
747 on model's output.  
748



## UniChill model



**PGC model**

