

Process-based models outcompete correlative models in projecting spring phenology of trees in a future warmer climate

Daphné Asse, Christophe Randin, Marc Bonhomme, Anne Delestrade,

Isabelle Chuine

▶ To cite this version:

Daphné Asse, Christophe Randin, Marc Bonhomme, Anne Delestrade, Isabelle Chuine. Processbased models outcompete correlative models in projecting spring phenology of trees in a future warmer climate. Agricultural and Forest Meteorology, 2020, 285-286, 24 p. 10.1016/j.agrformet.2020.107931 . hal-02886518

HAL Id: hal-02886518 https://hal.science/hal-02886518

Submitted on 2 Dec 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers. L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1	Process-based models outcompete correlative models in projecting spring
2	phenology of trees in a future warmer climate
3	Running title: Correlative vs process-based phenology models
4	Authors: Daphné Asse ^{1,2,3*} , Christophe F. Randin ^{2†} , Marc Bonhomme ⁴ , Anne Delestrade ¹ ,
5	Isabelle Chuine ^{3†}
6	
7	Adresses:
8	¹ Centre de Recherches sur les Ecosystèmes d'Altitude, Chamonix Mont-Blanc, France
9	² Department of ecology and Evolution, University of Lausanne, Switzerland
10	³ Centre d'Ecologie Fonctionnelle et Evolutive, UMR 5175, CNRS- Université de Montpellier - Université Paul-
11	Valéry Montpellier – EPHE. 1919 route de Mende, Montpellier F-34293 cedex 05, France
12	⁴ Université Clermont Auvergne, INRA, UMR 547 PIAF, Clermont-Ferrand F-63100, France
13	
14	*First and corresponding author: daphne.asse@gmail.com
15	[†] Lead author
16	
17	Corresponding authors:
18	Isabelle Chuine, tel. +33 467 613 279, fax +33 467 613 336, e-mail:
19	isabelle.chuine@cefe.cnrs.fr, postal address: CEFE, 1919 route de Mende, F-34293
20	Montpellier cedex 05
21 22	Christophe Randin, tel. +41 21 316 99 91, e-mail: christophe.randin@unil.ch, postal address: DEE UNIL, Biophore, CH-1015 Lausanne

- 24 Abstract: 330 words
- 25 Main text: 7323 words
- 26 Number of figures: 7
- 27 Number of tables: 1

29 Abstract

30

31 Many phenology models have been developed to explain historical trends in plant 32 phenology and to forecast future ones. Two main types of model can be distinguished: 33 correlative models, that statistically relate descriptors of climate to the date of occurrence of a 34 phenological event, and process-based models that build upon explicit causal relationships 35 determined experimentally. While process-based models are believed to provide more robust 36 projections in novel conditions, it is still unclear whether this assertion always holds true and why. In addition, the efficiency and robustness of the two model categories have rarely been 37 38 compared.

Here we aimed at comparing the efficiency and the robustness of correlative and process-based phenology models with contrasting levels of complexity in both historical and future climatic conditions. Models were calibrated, validated and compared using budburst dates of five tree species across the French Alps collected during 8 years by a citizen-science program.

Process-based models were less efficient, yet more robust than correlative models, even when their parameter estimates relied entirely on inverse modeling, i.e. parameter values estimated using observed budburst dates and optimization algorithms. Their robustness further slightly increased when their parameter estimates relied on forward estimation, i.e. parameter values measured experimentally. Our results therefore suggest that the robustness of process-based models comes both from the fact that they describe causal relationships and the fact that their parameters can be directly measured.

51 Process-based models projected a reduction in the phenological cline along the 52 elevation gradient for all species by the end of the 21st century. This was due to a delaying

effect of winter warming at low elevation where conditions will move away from optimal chilling conditions that break bud dormancy *vs* an advancing effect of spring warming at high elevation where optimal chilling conditions for dormancy release will persist even under the most pessimistic emissions scenario RCP 8.5.

57 These results advocate for increasing efforts in developing process-based phenology 58 models as well as forward modelling, in order to provide accurate projections in future 59 climatic conditions.

60

61

Key words: Budburst, elevation gradients, Alps, citizen science, endodormancy release,
 climate change impact

1. Introduction

67 Phenology is a key aspect of plant and animal life strategies because it determines the 68 timing of growth and reproduction. Life cycle of species must be adapted to the local weather 69 conditions and resources. As a consequence, phenology is one of the top controls of crop 70 vield (Olesen et al., 2011; Nissanka et al., 2015), population dynamics (Anderson et al., 71 2013), species distribution (Chuine, 2010) and evolutionary dynamics (Duputié et al., 2015; 72 Burghardt et al., 2015). Phenology also ultimately regulates many functions of ecosystems 73 such as productivity (Richardson et al., 2012), ecosystem carbon cycling (Delpierre et al., 74 2009), water (Hogg et al., 2000) and nutriment cycling (Cooke and Weih, 2005).

75 Since the 1970s, spring phenology has been reported to advance in response to 76 warming (Walther et al. 2002; Parmesan and Yohe, 2003; Menzel et al. 2006; Fu et al. 2014). 77 For instance, it has been shown that the apparent response of leaf unfolding to temperature 78 was -3.4 days per °C between 1980 and 2013 in temperate Europe (Fu et al., 2015). This 79 advance in spring phenology events is due to the warming of springs as bud growth rate is 80 positively and strongly related to temperature (see for review Chuine and Régnière, 2017). 81 However, this trend has been slowing down by about 40% after 2000 (Fu et al., 2015). One of 82 the most likely hypotheses to explain this slowdown is the warming of winters (Asse et al., 83 2018). Indeed, most of temperate and boreal trees have developed a key adaptation to winter 84 cold: the inability to resume growth despite transient favorable growing conditions in terms of temperature (Howe et al., 2000). This particular physiological state, called endodormancy 85 86 (Lang et al., 1987), establishes in fall and disappears in early to late winter after a certain 87 exposure to cold temperatures. Therefore, the warming of winters is suspected to delay 88 endodormancy release and be responsible for the apparent decrease in the response of leaf

unfolding to warming after 2000. Ultimately, this lack of chilling temperatures might compromise budburst itself at some point if warming continues (Chuine et al., 2016). Such a situation is more likely to occur in populations inhabiting the warm edge of a species range and/or lower elevations in mountain regions, where species are already in suboptimal chilling conditions (Benmoussa et al., 2018; Guo et al., 2015). More than ever there is a need for more accurate projections of tree phenology for the upcoming decades to remove the large uncertainties that still remains.

96 Two main categories of predictive phenology models exist although there can be a 97 continuum in-between: correlative and process-based models (for review see (Chuine et al., 98 2013; Chuine and Régnière, 2017). Correlative models statistically relate descriptors of 99 climate to phenological variables (i.e. usually the occurrence dates of a phenological phase 100 such as bud break or flowering). In correlative models, parameters have no a priori defined 101 ecological meaning and processes can be implicit (process-implicit) (Lebourgeois et al., 102 2010). In contrast, process-based models are built around explicitly stated mechanisms and 103 parameters have a clear ecological interpretation that is defined *a priori*. In this category of 104 model, response curves are often obtained directly from experiments, contrasting with 105 empirical relationships of correlative models. Consequently, process-based models often 106 require a larger number of parameters to be estimated or measured, with the consequence of a 107 higher level of complexity than correlative models. However, they provide greater insights 108 into how precisely each driver affects the trait, and they are expected to provide more robust 109 projections in new climatic conditions corresponding either to other geographical areas or 110 other time periods (Chuine et al., 2016).

111 Among the most widely used process-based phenology models, are the so-called 1-112 phase models that describe solely the ecodormancy phase, which follows the endodormancy 113 phase. During the ecodormancy phase, bud cell elongation can take place whenever 114 temperatures are appropriate, and the higher the temperature is, the higher is the rate of cell 115 elongation during this phase. This category of models has been shown to be efficient in 116 predicting accurately budburst date under historical climate (Vitasse et al., 2011; Basler, 2016). Another category of models, called 2-phase models, describes additionally the 117 118 endodormancy phase, and take into account the possible negative effect of winter warming on 119 endodormancy release. This category of models is thus considered to provide more accurate 120 projections in future climatic conditions (Chuine, 2010; Vitasse et al., 2011). However, it has 121 been shown recently that this second type of models might suffer from flawed parameter 122 estimation when dates of endodormancy release have not been used for their calibration 123 (Chuine et al., 2016). Unfortunately, observations of endodormancy release date are very rare 124 because they are very difficult to determine (Jones et al., 2013; Chuine et al., 2016). Models 125 are thus usually calibrated using solely bud break or flowering dates (Chuine, 2000; Caffarra 126 et al., 2011; Luedeling et al., 2009; but see Chuine et al., 2016). Some other models go 127 further in the description of the processes by integrating a photoperiod cue (Schaber and 128 Badeck, 2003; Gaüzere et al., 2017). Some studies indeed support the hypothesis that in 129 photosensitive species, which might represent about 30% of temperate tree species (Zohner et al., 2016), long photoperiod might compensate for insufficient chilling (Caffarra et al., 130 131 2011a; Gaüzere et al. 2017).

There is now a large number of phenology models that differ in their level of complexity and in the types of response function to environmental cues they use (see for review Chuine *et al.*, 2013; Basler, 2016; Chuine and Régnière, 2017). However, very few 135 studies aimed at comparing their efficiency and robustness so far (Basler, 2016), especially in 136 future climatic conditions (but see Vitasse et al., 2011; Chuine et al., 2016; Gaüzere et al., 137 2017), while this has been done multiple times for species distribution models (e.g. Cheaib et 138 al., 2012; Higgins et al., 2012; Morin and Thuiller, 2009; Kearney et al., 2010) and crop 139 models (Lobell and Burke, 2010) for example. By efficiency, we mean here the ability of the 140 model to provide accurate predictions in conditions that have been used to calibrate the model (Janssen and Heuberger, 1995); and by robustness, we mean here the ability of the model to 141 142 provide accurate predictions in external conditions (Janssen and Heuberger, 1995), i.e. other conditions than those used to calibrate the model. Model's robustness determines its 143 144 transferability in time and space.

145 Process-based models are usually expected to provide more accurate projections for 146 the future than correlative models because they describe causal relationships. The effect of 147 each driver identified as affecting a particular trait value can be described by a causal relationship, sometimes involving other drivers as well (interaction between drivers). For this 148 149 reason, process-based models have also an expected greater potential to deal with non-analog 150 situations. However, the putative higher robustness of process-based models could also come 151 from the fact that parameter values describing the causal relationships, or at least some of 152 them, can be measured directly (forward estimation of parameter values) instead of being 153 inferred statistically through inverse modelling techniques and data assimilation (backward 154 estimation of parameter values). Yet, there has been no attempt so far to validate this widely 155 accepted expectation.

Here, we aimed at comparing the efficiency and robustness of correlative *vs* processbased phenology models with contrasting levels of complexity, both in space and time. More

precisely, we aimed at answering the following questions: (1) Are process-based phenology models more robust than correlative models? (2) If so, is it because they describe causal relationships or because they can be less dependent on statistical inference (i.e. back estimation of parameter values) and rely more on experimental measurements (i.e. forward estimation of parameter values)? (3) How do projections of both types of model differ in future climatic conditions?

Using observations of budburst dates collected over the Western Alps by a citizen science program during 8 years, and experimental data, we calibrated correlative and processbased phenology models with three levels of complexity for five major tree species: *Corylus avellana* (L.), *Fraxinus excelsior* (L.), *Betula pendula* (Roth), *Larix decidua* (Mill.) and *Picea abies* (L.). We then compared their predictions and projections over the Western Alps in historical climate and in future climate respectively.

170 The Western Alps are particularly interesting to evaluate phenology models because the elevation gradient provides a wide temperature range on a very short distance. In addition, 171 172 the southern part of the Western Alps is nearly located at the warmest edge of the geographic 173 range of the five studied species, where it has been shown that winter warming is already 174 affecting endodormancy release and budburst (Asse et al., 2018). Finally, temperature has already increased in the Western Alps twice as fast as in the northern hemisphere during the 175 20th century (Rebetez and Reinhard, 2008) and recent evidence indicates that the current 176 warming rate increases with increasing elevation (Mountain Research Initiative EDW 177 178 Working Group, 2015). Consequently, mountain summits might warm faster than lower 179 elevation sites, so that the response of mountain ecosystems to climate change might be non180 linear along elevation gradients. Therefore, ultimately, we aimed at answering a fourth181 question: (4) How will climate change alter the budburst date of alpine species?

183 **2. Methods**

184 2.1. Phenological and meteorological data

We used observations of the budburst date, defined as the first day when 10% of 185 vegetative buds of a given individual tree are opened (BBCH 07), of five common tree 186 species: ash (Fraxinus excelsior L.), birch (Betula pendula Roth), hazel (Corvlus avellana 187 L.), larch (Larix decidua Mill.), and spruce (Picea abies L.). These species show different 188 189 elevation ranges (from 150 - 1300 m a.s.l. for Corylus to 700 – 2100 m a.s.l for Larix), which allowed us to compare the two types of model over a large climatic gradient. The data were 190 191 extracted from the Phenoclim database of CREA (Centre de Recherches sur les Ecosystèmes 192 d'Altitude, Chamonix, France) (www.phenoclim.org) which covers the entire French Alps (for further details of the Phenoclim protocol see Appendix A) (Fig. 1). In total, and 193 194 irrespective of species, 242 sites were surveyed for budburst between 2007 and 2014.

Sixty of the observation sites (ranging from 372 to 1919 m a.s.l,) were equipped with 195 196 meteorological stations that recorded air temperature at 2-m height every 15 min with a 197 DA8B20 digital thermometer placed in a white ventilated plastic shelter (Dallas Semiconductor MAXIM, "http://www.maxime-ic.com", operating range of -55 to 125 °C 198 and an accuracy of 0.5 °C over the range of -10 to 85 °C) (Fig. 1). These data were used to 199 200 calculate the daily mean air temperature at the sixty sites and were also interpolated at 201 observation sites without meteorological stations using a 25-m digital elevation model 202 (DEM) as follows. We first constructed a linear model of daily temperature at 2-m height as a function of elevation. Residuals of this linear model were then interpolated using the 203 204 calibrations points over the entire French Alps according to the inverse distance weighted 205 algorithm (IDW; see also: Kollas et al., 2014; Cianfrani et al., 2015, for further details).

206

In addition to Phenoclim data, we used data from an experiment on Larix decidua

realized at INRA UMR PIAF (Clermont-Ferrand, France) during winter 2010-2011. The aim 207 of this experiment was to determine the date of endodormancy release, the chilling required 208 209 to break endodormancy and the response of bud growth to temperature during the ecodormancy phase of Larix decidua Mill. In a first experiment, 60 twigs of 30 to 40 cm, 210 were sampled on 4 sites (Saulzet, Orcival, Lamartine, Laqueuille) on February 2nd and 211 212 immediately taken to the laboratory. Twigs were recut under water and put in flasks filled up with water. Water was subsequently changed twice a week. Twigs were divided into six sub-213 214 sets that were placed in growth chambers (Sanyo MLR 351H) which were set to: 25, 20, 15, 215 10, 5, 2°C with 16h photoperiod and a light intensity of 50 µE/m2/s, relative humidity (RH) 216 of 70%, except for the 5°C and 2°C chambers which received 20 µE/m2/s and RH 50%. This 217 experiment was designed to investigate the response to temperature of bud growth during the 218 ecodormancy phase. In a second experiment, 5 twigs were sampled on 5 trees of Larix 219 decidua Mill. from the end of September to early February on the same 4 sites at ten dates: 27 220 Sep; 18 Oct; 17 Nov; 14 Dec; 29 Dec; 04 Jan; 11 Jan; 18 Jan; 24 Jan; 02 Feb. Twigs were recut under water and put in flasks filled up with water. Water was subsequently changed 221 222 twice a week. Twigs were placed in growth chambers (Sanyo MLR 351H) at 20°C, 16h 223 photoperiod, 50 µE/m2/s, RH 70%. This experiment was designed to determine the 224 endodormancy release date and the chilling required to break endodormancy. In the two 225 experiments, each bud of each twig was monitored every second day to determine the date of 226 budburst (BBCH 07).

227

228 2.2. Correlative phenology model

We used mixed-effects models for each of the five species with budburst dates as response variables and with growing degree-days and chilling as predicting variables (Asse *et*

al. 2018). We defined chilling for each species and each observation site as the frequency of 231 days with a daily temperature $< 5^{\circ}$ C from September 1st to December 31st of the calendar 232 233 year preceding budburst (Dantec et al., 2014). We then calculated for each species and each observation site growing degree-days (GDD) defined as the sum of positive daily mean 234 temperature from January 1st to the median date of budburst observed over the 2007-2014 235 236 observation period. GDD was calculated with two different temperature thresholds: the more commonly-used 5°C (hereafter designated as GDD5) and 0°C (hereafter designated as 237 GDD0) because daily mean temperatures between 0 and 5°C may contribute to trigger 238 239 budburst events in plants growing in mountainous environments (Körner 1999; Vitasse et al. 2016). We chose Jan 1st as the starting date of accumulation because the ecodormancy phase 240 241 can begin as early as January for some species and because the climatic conditions at the beginning of this phase vary a lot between species, years, and sites along elevation and 242 243 latitudinal gradient (Asse et al., 2018).

244

245 2.3. Process-based phenology models

We used several process-based phenology models to simulate the budburst dates of each species.

First, we used 1-phase models, that describe the ecodormancy phase only and assume that endodormancy-release always occurs before temperature can trigger cell elongation and that there is no effect of chilling on forcing requirement (Chuine et al., 2013). Budburst occurs at t_f when the sum of the daily rates of development (R_f) reaches the critical value F^* :

$$\sum_{t_0}^{t_f} R_f(T_d) \ge F^* \tag{1}$$

with t_0 the starting date of forcing and T_d the daily mean temperature.

- We used several versions of the model that differed by the response function to temperature (R_f), which determines the daily rate of bud development:
- the Growing Degree Day function, similarly to the correlative models,

256
$$R_f(T_d) = Max(0; T_d - T_b)$$
 (2)

257 with T_b the lower threshold temperature;

and two more complex functions: the sigmoid function,

$$R_f(T_d) = \frac{1}{1 + e^{-d_T(T_d - T_{50})}}$$
(3)

259 with d_T the steepness of the response and T_{50} the mid-response temperature;

and the Wang function (Wang and Engel, 1998)

261
$$R_{f} = Max \left[\left(2(T_{d} - T_{min})^{\alpha} \left(T_{opt} - T_{min} \right)^{\alpha} - \frac{(T_{d} - T_{min})^{2\alpha}}{(T_{opt} - T_{min})^{2\alpha}} \right), 0 \right]$$
(4)

262 with
$$\alpha = \ln(2) / \ln\left(\frac{T_{max} - T_{min}}{T_{opt} - T_{min}}\right)$$
, and T_{min} , T_{max} and T_{opt} the cardinal temperatures.

These models have from 3 to 5 parameters that were either calibrated using inverse modelling techniques or prescribed using experimental data (see 2.4).

Second, we used sequential 2-phase models (Hanninen, 1987) that take into account chilling requirements during the endodormancy phase (first phase) and forcing requirements during the ecodormancy phase (second phase; Chuine et al., 1999). The endodormancy phase ends at t_c when the accumulation of the daily rates of dormancy release (R_c) reaches the critical sum of chilling units C^* :

270
$$\sum_{t_0}^{t_c} R_c(T_d) \ge C^*$$
 (5)

271 From t_c to t_f (date of budburst), forcing units are then accumulated as:

272
$$\sum_{t_c}^{t_f} R_f(T_d) \ge F^*.$$
 (6)

We used several versions of the model that differed by the response function to temperature during the endodormancy phase (R_c) that determines the daily rate of endodormancy release:

the Wang function (Eq. 4) and a simple lower threshold function,

277
$$R_c(T_d) = \begin{cases} 1 & \text{if } T_d < T_h \\ 0 & \text{if } T_d \ge T_h \end{cases}$$
(7)

For the ecodormancy phase we used the best R_f function found with the 1-phase model for each species. These 2-phase models have 6 to 8 parameters that were either calibrated using inverse modelling techniques or prescribed using experimental data.

281

282 2.4 Parameter value estimation

283 The data set was divided into several data subsets: data subset 1 corresponded to data 284 collected on sites equipped with a meteorological station; data subset 2 corresponded to data 285 collected on sites not equipped with a meteorological station; data subset 3 corresponded to 286 data from observation sites East of a species-specific longitudinal threshold; data subset 4 287 corresponded to data from observation sites West of this threshold. The species-specific longitude corresponded to the longitude on both sides of which the species was equally 288 289 present (i.e. 50% of the observation sites West of the longitude and 50% East of the longitude). The data subsets contained a similar number of data ($\overline{\sigma}$ =12). 290

First, all models were calibrated using the phenological data and corresponding meteorological data of data subset 1. The best models obtained were then additionally calibrated twice using data subset 3 and data subset 4 (Fig. 1). The three different calibrations aimed at evaluating the transferability of the models to conditions that differ from those used to calibrate the models (see section 2.6.1).

Correlative phenology models which corresponded to mixed effects models were 296 297 generated in R (version 3.3.2; R Core Team, 2016) using the library nlme (Lindstrom & 298 Bates 1990; Pinheiro & Bates 1996) with observation sites as random effect. Indeed, there 299 may be some site-specific adaptations, which would blur an overall relationship between the 300 temperature-based predicting variables (i.e chilling, GDD) and budburst. We considered 301 models with all combinations of the two predicting variables (i.e. chilling and GDD), 302 including also univariate models. GDD with two different thresholds were tested separately 303 but in combination with chilling in multivariate models.

Process-based models were adjusted by minimizing the residual sum of squares using the simulated annealing algorithm of Metropolis (Chuine et al., 1998) using the Phenology Modelling Platform software (PMP5; http://www.cefe.cnrs.fr/fr/recherche/ef/forecast/phenology-modelling-platform) (Chuine et al., 2013). Adjustment was repeated 20 times to assure that the global optimum had been reached.

Finally, we also used the experimental observations on *Larix* to constrain the calibration of the best 2-phase model. Using the results of the two experiments, we were able to estimate the critical sum of chilling during the endodormancy phase (C^*), the response function to temperature (R_f) and the critical value F^* of the ecodormancy phase. We thus fixed C^* , the parameter values of the R_f function and F^* to those estimates. This model is 315 called hereafter "forward calibrated model".

316

317 2.5. Model comparison

Models were compared using four performance indices: adjusted R-square, Akaike's Information Criterion corrected for small sample size (AIC_C) (Burnham and Anderson, 2002); the efficiency (EFF) (Nash and Sutcliffe, 1970); the root mean square error for the calibration (RMSE) and validation (RMSE_P) data sets respectively, the systematic root mean square error (RMSEs) that estimates the model linear error (or bias).

AICc =
$$N \times ln\left(\frac{\sum_{i=1}^{n} (O_i - P_i)^2}{N}\right) + 2k + \left(\frac{2k(k+1)}{N - K - 1}\right)$$
 (8)

323

$$EFF = 1 - \frac{\sum_{i=1}^{n} (O_i - P_i)^2}{\sum_{i=1}^{n} (O_i - \overline{O}_i)^2}$$
(9)

324

325
$$\operatorname{RMSE}_{P} \text{ or } \operatorname{RMSE} = \sqrt{\frac{\sum_{i=1}^{n} (O_i - P_i)^2}{n}}$$
(10)

326

$$\text{RMSEs} = \sqrt{\frac{\sum_{i=1}^{n} (O_i - \hat{P}_i)^2}{n}}$$
(11)

where O_i represents observed dates, P_i represents projected dates, \hat{P}_i represents regressed prediction dates and N or n is the number of observations and k is the number of parameters. We also used the ratio of performance to interquartile distance (RPIQ) that takes both the prediction error and the variation in observed values into account (Bellon-Maurel et al., 331 2010). The greater the RPIQ, the better the model's predictive capacity.

332
$$\operatorname{RPIQ} = \frac{(Q3-Q1)}{RMSE_p}$$
(12)

where *Q1* represents the value below which we can find 25% of the sample and *Q3* represents
the value below which we find 75% of the sample.

Based on the AICc, EFF, RMSE, RMSEs, RPIQ and R² (adjusted R-squared), we first selected the best correlative model with GDD as variable, the best correlative model with GDD and chilling as variables, and the best 1-phase and 2-phase models. We additionally bootstrapped the best models (with 999 repetitions) to assess the effect of sampling bias on RMSE indices, a good overall measure of model performance. We then calibrated linear regressions of the model residuals (observed dates – predicted dates) as a function of elevation.

342 We additionally tested the performance of the two types of process-based model in 343 usual vs unusual climatic conditions. We identified two climatically contrasted years over the 344 observation period. First, a typical year with cold temperature during the fall and the early 345 winter (called hereafter for the sake of simplicity winter period) followed by warm 346 temperature during the late winter and the early spring (called hereafter for the sake of 347 simplicity "preseason period"). Second, an unusually warm year with a warm winter period 348 followed by a warm preseason period. Winter period corresponds to the development phase 349 of endodormancy and preseason period corresponds to the development phase of ecodormancy. To identify the three climatically contrasted years, we compared quantile 350 351 values of chilling and GDD between years for each species calculated as defined above.

352

353 2.6. Model projections

Following Bray & Storch (2009), we use the term "prediction" to refer to outputs of models corresponding to the conditions used for the calibration; and the term "projection" to refer to outputs of models corresponding to conditions not used for the calibration. The term "prediction" conveys a sense of certainty, while the term "projection" conveys a sense of possibility.

359

360 2.6.1. Projections across space

361 We performed three spatial cross-validations to assess the transferability of the best 362 models to a wider geographic area. First, we used models calibrated on observation sites with 363 meteorological stations (data subset 1) to project the budburst date at observation sites without meteorological stations (data subset2) using interpolated 2-m temperature for the 364 365 2007-2014 time period (see section 2.1). Second, we used models calibrated on observation sites West of the species-specific longitude (data subset 3) to project the budburst date on 366 observation sites East of this longitude (data subset 4), and vice versa. The evaluation of the 367 368 models' performance with data subsets 3 and 4 provides a more robust estimation of their transferability compared to data subsets 1 and 2 because of the lower auto-correlation of the 369 meteorological conditions between them. 370

The accuracy of the projections was estimated using RMSE_P, RMSE_S, RPIQ and R². We additionally bootstrapped models (with 999 repetitions) to assess the effect of sampling bias on RMSE indices. We finally calibrated linear regressions of the model residuals (observed dates – projected dates) as a function of elevation.

375

376 2.6.2. Projections across time using climate scenarios

377 We compared the projections of the best models calibrated on observation sites with 378 meteorological stations, in historical (1950-2005) and future climatic conditions (2006 to 379 2100). We used the climatic data generated by the ALADIN-Climat v5 RCM model (CNRM) 380 for the CMIP5 experiment at a 12-km resolution and downscaled at 8-km resolution using 381 quantile-quantile method (http://drias-climat.fr/). For the future period (2006-2100), we used 382 the scenario RCP8.5. We chose a single scenario because our objective here was to realize a sensitivity analysis of the different model types to climate change and not to provide impact 383 384 projections. However, we chose the RCP 8.5 scenario because it is close to the current trajectory. Daily minimum and maximum temperatures were extracted for the grid covering 385 the French Alps (43°48'N to 46°47'N, 5°59'E to 7°09'E). We compared the budburst dates 386 387 projected by the best models for two different elevation ranges whose limits depended on the 388 species distribution according to the CBNA (Conservatoire Botanique National Alpin) 389 database.

The annual shift of projected budburst dates was calculated as the Sen's estimator of the slope of regressions (Sen, 1968) between projected budburst dates and years over the period 1950 to 2100. The shift in the budburst date over this period was also calculated.

Budburst dates projected by each model over the 1950-2100 time period were plotted with the associated confidence interval derived from the external validation (see section 2.5.1.). The annual / decadal shift of projected budburst dates from Sen's estimator of slope was additionally provided for each model type and each of the 8-km cells in the French Alps for the same 1950-2100 period.

398 The different models that were compared and the different calibrations, validations 399 and projections that were realized are summarized in Table 1.



0 — 50 km

402 Fig. 1: Locations of the data used for the study. Map showing the location of the study area 403 (western part of the Alps) at the scale of Europe (a). Maps showing the location of sites with 404 phenological records for the five species in the Western Alps (b-f): Betula pendula (birch) (b), 405 Corvlus avellana (hazel) (c), Fraxinus excelsior (ash) (d), Larix decidua (larch) (e), Picea abies 406 (spruce) (f). Sites without meteorological station are shown with filled white circles and sites with 407 meteorological station are shown with filled black triangles. The dotted lines correspond to the 408 species-specific longitudes separating West and East sites that defined the sub-datasets for each 409 species (see section 2.4).

410

411

Models compared													
Model type		С	orrelativ	ve					Pro	ocess-based			
Model family	sin	gle varia	able	biva	riate		1-	phase		2-р	hase		Forward calibrated 2-phase
Temperature response	GDD	GDD	TL	GDD +TL	GDD+ TL	GDD	sign	noid	Wang	TL + sigmoid	Wa sigr	ng + noid	TL + sigmoid
Parameter values of the response	Tb=0	Tb=5	Tb=5	Tb=0; Th=5	Tb=5; Th=5				fitted				C*=58.1; F*=7.4
Model calibration: best c	orrelativ	e, 1-pha	ase, 2-pl	nase mo	dels + fo	orward	calibr	ated r	nodel				-
Calibration datasets					mete	o sites		ea	st sites	west site	es		
Time period							2	007-2	014				
Model validation: best co	rrelative	e, 1-pha	se, 2-ph	ase mo	models + forward calibrated model								
Validation datasets (acros	s space)			no meteo sites west sites east sites									
Time period		2007-2014											
Model projection: best co	orrelativ	e, 1-pha	ise, 2-ph	iase mo	dels + fo	orward o	calibra	ated n	nodel				
Projection dataset (across	time)			AL 8k	ADIN-Cli m resolu	imat v5 ition	RCM	mode	l (CNRM) v	with RCP 8.5	5 at		
Time period							1	950-2	100				

Table 1: Summary of the different models that were compared and the different calibrations, validations and projections that were realized. GDD is the abbreviation of growing degree day function and TL of the threshold lower function. Meteo sites correspond to sites equipped with a meteorological station, no meteo sites corresponds to sites not equipped with a meteorological station, east sites correspond to observation sites East of a species-specific longitudinal threshold, west sites correspond to observation sites West of this threshold.

421 **3. Results**

422 *3.1. Selection of the best models*

423 Mixed effects models which best explained budburst dates were generally models including GDD5, and chilling as predicting variables (Appendix B). However, budburst dates 424 425 of Corvlus and Fraxinus were best explained by GDD0 together with chilling. Variance 426 partitioning also indicated an important joint contribution of GDD0 or GDD5 and chilling for 427 all species (Appendix B). However, over all 8 years and all locations, chilling did not explain 428 a significant part of the variance in spring phenology once forcing temperatures were taken 429 into account except in *Picea* (Appendix B). For further analysis we only present the results of 430 the correlative model with GDD0 or GDD5 (depending of the species) and chilling as 431 variables.

The response function to temperature in process-based models that best explained the budburst date was the lower threshold function for *Fraxinus* and *Picea* and the Wang function for the three other species for the endodormancy phase; and the sigmoid function for all species for the ecodormancy phase (Appendix C). However, because the differences in efficiency and AICc were very small between models using the Wang function and the threshold function, we selected the lower threshold function for all species for the rest of the analyses, for the sake of parsimony.

Process-based models performed the best for *Picea* and *Betula* (Fig. 2, Appendix D, Appendix F and Appendix G). However, model error increased with the distance to the mean budburst date, irrespective of the model and the species, with a tendency towards exaggerating early and late budburst dates (predicted dates too early or too late, respectively) (Appendix F and Appendix G). We found no trend in model residuals (observed – predicted

dates) along elevation, except for *Larix* for which observed budburst dates tended to occur
earlier than predicted by the models at low elevation and reversely at high elevation
(Appendix H and Appendix I).

447 All performance indices indicated that correlative models predicted the budburst date 448 more accurately than process-based models whatever the calibration dataset for all species (Appendix D). This result was confirmed by bootstrapped values of RMSE that were 449 450 significantly lower for correlative models than process-based models for all species (Fig. 2). 451 Performance indices were only slightly better for 2-phase models than 1-phase models (Fig. 2, Appendix D). However, comparing the performances for an unusually warm year, i.e. with 452 453 warm winter and warm preseason, we found that 2-phase process-based models performed 454 better for Corylus and Picea (Fig. 3). For the other species, model performance was similar 455 between the one- and 2-phase process-based models. For a typical year with a cold winter and 456 a warm preseason, performance indices were similar between the two types of process-based 457 model for all species (Fig. 3).

458

459 *3.2. Model transferability in space*

Whatever the validation data subset, process-based models provided more accurate projections of the budburst date than correlative models, except for *Picea abies* for which models' performed similarly (Fig. 2, Appendix E). Performances were similar between 2phase models and 1-phase models. Process-based models were thus more robust than correlative models. Indeed, while RMSE increased from predictions to projections in correlative models, they remained similar in process-based models (Fig. 2, Appendix E). Therefore, model performance of process-based models was more stable (3.45 and 0.87 mean 467 difference in RMSE between calibration and validation for the correlative and process-based468 models respectively).

469 Similarly to the predicted dates, error in projected dates increased with the distance to
470 the mean budburst date, irrespective of the model and the species (Appendix F and Appendix
471 G) with exaggerating early and late dates.

472 Model residuals were linearly related to elevation for *Corylus* and *Fraxinus*473 (correlative models only), and *Larix* (all models), with dates projected slightly too late at low
474 elevation and too early at high elevation (Appendix H and I).

475

476 *3.3. Projections of the budburst date in future climatic conditions*

477 *Evolution across time*

We compared the projections of the budburst date of the five species by the best correlative model and the best process-based 1-phase and 2-phase models over the historical period and the 21st century in the French Alps using climatic data simulated by the ALADIN-Climat RCM. Uncertainties in the climatic data (minimum temperatures, maximum temperatures) were similar along the period and should not therefore add a bias across time in the model projections (Appendix J).

Model projections differed substantially according to elevation and time period. At low elevation, up to 2050, correlative models and 1-phase models projected a continuous trend for earlier budburst dates -0.08 to -0.16 days/year and -0.09 to -0.12 days/year respectively; Fig. 4 & 5, Appendix K) while 2-phase models showed a much weaker trend for earlier budburst dates (-0.05 to -0.07 days/year; Fig. 4, Appendix K). Models projection diverged substantially after 2050. While correlative models projected still earlier budburst

dates (-0.27 to -0.48 days/year; Fig. 4, Appendix K), trend weakened in 1-phase models
projection (-0.03 to -0.20 days/year; Fig. 4, Appendix K); and vanished or even reverted in 2phase models projection (-0.01 to +0.16 days/year; Fig. 4, Appendix K).

493 At high elevation, correlative models provided astonishing projections with very low 494 interannual variability of budburst dates, a slight trend towards earlier date from 1950 to 2050 495 (-0.005 to -0.07 days/year; Fig. 4, Appendix K) that steepened after 2050 (-0.13 to -0.28 496 days/year; Fig. 4, Appendix K). Process-based models showed a trend for earlier budburst dates (-32 to -46 days) all along the 1950-2100 period. 1-phase models and 2-phase models 497 498 both projected a remarkably similar trend towards earlier budburst dates all along the 499 historical period and until 2050 (-0.16 to -0.21 days/year; Fig. 4, Appendix K). However, 500 while after 2050, the trend towards earlier budburst dates remained similar between the two 501 process-based models for Larix (-0.42 days/year) and Picea (-0.32 days/year), it weakened in 502 the 2-phase model for the other species (Fig. 4, Appendix K).

For *Fraxinus*, *Betula* and *Picea*, 2-phase models episodically projected budburst failure due to endodormancy release failure because of a lack of chilling. This situation occurred especially at low elevation and with an increasing frequency along the 21th century (Fig. 5).

507

508 Variation across space

509 Correlative models projected earlier budburst dates over the French Alps at an 8-km 510 resolution with a trend more pronounced in the outer and southern Alps than in the central 511 Alps where the elevation is higher on average. The contrast between outer and central Alps 512 was the most pronounced for *Betula*, *Larix* and *Picea* (Fig. 6). Reversely, 1-phase and 2-

513 phase models projected a steeper trend towards earlier budburst dates in the central Alps than 514 the outer Alps. However, contrary to 1-phase models, 2-phase models projected later dates in 515 the southern Alps for all species, and also in the north of the outer Alps for *Larix* and *Picea* 516 (Fig. 6). The contrasted projections between the outer and central Alps were more 517 pronounced for *Larix* (Fig. 6).

518

519 *3.4. Performance of the forward calibrated model*

520 The forward calibrated 2-phase model for Larix performed the worst on average compared to other models in predicting the budburst date whatever the calibration data subset 521 522 (Fig. 2, Appendix D), but nevertheless provided more accurate predictions of early dates than 523 the 2-phase model calibrated with inverse modelling (Appendix L). The model also provided 524 the most accurate projections for the sites without meteorological stations, but not for the 525 other data subsets (Fig. 2, Appendix E). More interestingly, this model was the only one to 526 provide a lower error on average with the validation data subsets than with the calibration data subsets (-0.39 vs +0.65 for 2-phase model and +0.84 for 1-phase model), and thus 527 528 showed the reverse behavior we usually observe with models of an increased error in external 529 (validation) conditions. Like other models (either correlative or process-based) for Larix decidua, residuals were linearly related to elevation, with projected dates tending to be 530 531 overestimated at low elevation and underestimated at high elevation (Appendix M).

532 Over the historical period and the 21st century, budburst dates projected by the 533 forward calibrated 2-phase model were very similar to those projected by the 2-phase model 534 either at low or high elevation (Fig. 7). However, the forward calibrated model showed much 535 more frequent endodormancy release failures than the 2-phase model which projected none 536 for *Larix* (Fig. 5 g, h). For this reason, we could not represent the shift of the budburst date

- 537 projected by the forward calibrated model for *Larix* over the French Alps for each grid cell
- 538 for the period 1950-2100 (Fig. 6).





540 Fig. 2: Boxplots of bootstrapped values of RMSE (days). Performance of the best models in predicting (a, c, e, g, i) and projecting the budburst date (b, d, f, h, j). Predictions correspond 541 542 to the budburst dates predicted by the models for their respective calibration dataset: sites 543 with meteorological stations (clear grey); sites West of the species-specific longitudinal 544 threshold (grey); sites East of the species-specific longitudinal threshold (dark grey). Projections correspond to budburst dates predicted by the three different versions of 545 546 calibrated models for respectively observation sites without meteorological stations (clear grey); observations sites East of the species-specific longitudinal threshold (grey); 547 observation sites West of the species-specific longitudinal threshold (dark grey). Models on 548 549 the X axis are the same calibrated models on right and left panels which differ only by the 550 datasets used to evaluate the model performance distinguished by the different shades of 551 grey. Correlative 1 refers to the linear mixed model with GDD only. Correlative 2 refers to the linear model with GDD and chilling as variables. PB 1-phase refers to the process-based 552 553 1-phase model. PB 2-phase refers to the process-based 2-phase model. Forward calibrated PB 554 refers to the forward calibrated process-based 2-phase model.





Fig. 3: Performance (Efficiency a, b; RMSE c, d) of the process-based models in predicting 558 559 the budburst date of the calibration data subset 1 (sites with meteorological stations) for a 560 year with a warm winter followed by a warm preseason (a, c) and a year with a cold winter 561 followed by a warm preseason (b, d). Process-based 1-phase models use a sigmoid function 562 of temperature for the ecodormancy phase. Process-based 2-phase models use a lower 563 threshold function of temperature for the endodormancy phase and a sigmoid function of 564 temperature for the ecodormancy phase. EFF, model efficiency; RMSE, roots-mean-squared error (days). Model labels as in Fig. 2. 565



Fig. 4: Budburst date projected by the correlative 2 model (with GDD and chilling as variables)
(blue), the process-based 1-phase (grey) and the process-based 2-phase model (red) in
historical climate and future climate according to scenario RCP8.5, in the Alps at low

- 573 elevation (a, c, e, g, i) and high elevation (b, d, f, h, j). Elevation limits depend on the species.
- 574 Low elevation: Corylus= 100 to 1000m asl.; Fraxinus= 100 to 1000 m asl.; Betula= 100 to
- 575 1000 m asl.; *Larix*= 400 to 1500 m asl. and *Picea*= 100 to 1500 m asl.. For high elevation:
- 576 *Corylus*= 1001 to 2000m asl.; *Fraxinus*= 1001 to 2000 m asl.; *Betula*= 1001 to 2300 m asl.;
- 577 Larix= 1501 to 2700 m asl. and Picea= 1001 to 2500 m asl.. Bold lines indicate the projected
- 578 mean date and areas indicate the confidence interval of the model. Model labels as in Fig. 2.





- 582 Fig. 5: Percentage of sites showing dormancy breaking failure under climate scenario
- 583 RCP8.5 in the Alps along the years (a, c, e, g, i) and along the elevation gradient (b, d, f, h, j).
- 584 Grey dots indicate values for the process-based 2-phase model and black dots indicate values
- 585 for the forward calibrated process-based 2-phase model. Note that the 2-phase process-based
- 586 model did not project dormancy breaking failure for *Larix decidua*. Model labels as in Fig. 2.



- 589 **Fig. 6:** Shift in budburst date projected by the correlative (with GDD and chilling as variables)
- 590 (a, d, g, j, m), the process-based 1-phase (b, e, h, k, n) and 2-phase (c, f, i, l, o) models in the
- 591 French Alps (spatial resolution: 8 km) between 1950 and 2100 (scenario RCP8.5). Shift was
- 592 calculated as the Sen's estimator of the slope of regressions between projected budburst dates
- and years over the period 1950 to 2100.



598 Fig. 7: Budburst date of *Larix decidua* projected by the 2-phase model (red) and the forward 599 calibrated 2-phase model (yellow) in historical and future climate (scenario RCP8.5) in the 600 Alps at low elevation (400 to 1500 m asl.) (a) and high elevation (1501 to 2700 m asl.) (b). Red curves indicate the mean date projected by the 2-phase model and red areas indicate the 601 confidence interval of the model. Brown curves indicate the mean date projected by the 602 603 forward calibrated model and orange areas indicate the confidence interval of the model. 604 Because the forward calibrated model showed much more frequent budburst failures due to 605 endodormancy release failures than the 2-phase model, we could not represent the deviation 606 of budburst date projected by the calibrated model over the French Alps for the period 1950-2100. Model labels as in Fig. 2. 607

- 608
- 609

610 4. Discussion

611 4.1. Process-based phenology models provide more robust projections than correlative612 models

613 Linear mixed models using chilling days and growing degree days (GDD) were more 614 efficient than process-based models in predicting the budburst date in calibration conditions (i.e. sensu Randin et al., 2006). However, process-based models were more efficient than 615 616 correlative models to project budburst date in external conditions (except for *Picea* for which the three model types revealed similar performance). Error in predicted dates and projected 617 618 dates increased with the distance to the mean budburst date of the calibration datasets, 619 irrespective of the model and the species. This error inflation at the edge of the calibration 620 range leads to exaggerating early and late dates. However, errors were lower for process-621 based models compared to correlative models probably because the former formalize causal 622 relationships between the dependent variable and the independent variables across the range 623 of projection contrary to the latter. Although, these conclusions are dependent on the models 624 we have used for this study the way we chose the models asserts a certain degree of 625 generality to these conclusions because models differed essentially by their structure and not by their predicting variables. 626

Projections of the forward calibrated 2-phase model were not more accurate than those of the other 2-phase models except for sites without meteorological stations. However, it was the only model that did not show an increased error in external conditions. Increased accuracy in this model was mainly achieved through a more accurate prediction of early dates. Our results show that robustness of process-based models can come additionally from forward parameter estimation, but also that forward parameter estimation is not necessarily 633 the Holy Grail that we should seek. Another study conducted on rice (Nagano et al., 2012; 634 but see Satake et al., 2013) showed that phenology models calibrated by forward estimation 635 actually might perform worse in situ conditions than in controlled conditions and vice versa. 636 This study suggests that either the effect of some abiotic factors and their interactions or the daily variation of these factors in nature might be poorly represented under controlled 637 638 conditions, and that epigenetic or acclimation effects might interfere. Besides this, results 639 from experiments can sometimes be biased by ontogenetic effects when young cohorts of 640 individuals are used (Vitasse, 2013). Thus, it seems that backward and forward parameter estimations have both biases that come from the same reason, i.e. incomplete sampling of the 641 642 environmental conditions that affect the phenology, wherever natural or artificial.

643 Therefore, obtaining realistic and accurate response curves of plant responses to 644 environmental cues might actually require a combination of both the experimental approach 645 (forward estimation) and the statistical approach (backward estimation), especially when for 646 the latter, calibration datasets are small and span short time periods or small geographical 647 areas. However, forward estimation of model's parameters requires costly equipment such as greenhouses or growth chambers for which temperature and light conditions can be 648 649 controlled. When forward estimation is impossible, backward estimation of parameter values 650 could nevertheless benefit from additional expert knowledge based on experimental grounds 651 already published in the literature (see for review Chuine and Régnière, 2017).

652

653 *4.2. Model transferability through time and space*

Divergence between projections of correlative and 2-phase models in future climatic
 conditions across the Alps are striking. For all species at high elevation over the 1950-2050

656 period, correlative models projected earlier dates than 2-phase models, while after 2050, projections were similar. Standard deviations of the projected dates before 2050 for 657 658 correlative models were also surprisingly small, particularly for Larix. This might be due to 659 the fact that the GDD variable was calculated over the same period of the year along the elevation gradient. At high elevation, GDD remains low every year, yielding a low variation 660 661 in the projected budburst dates, which was particularly marked during the historical period. 662 Because *Larix* is the species that reaches the tree line, variations of GDD are even lower for 663 this species compared to the four other species. These results highlight the limitations of 664 correlative models to simulate budburst dates when transferred to another spatial or temporal 665 domain.

666 Performance indices were similar between 1-phase models and 2-phase models for 667 predictions and projections in historical conditions, suggesting that so far chilling had no 668 major effect on the budburst date because it was sufficient to fully release endodormancy. 669 Consequently, this means that 1-phase models are complex enough to predict and project 670 budburst dates accurately in historical climatic conditions (Chuine et al., 1999; Linkosalo et al., 2008; Vitasse et al., 2011). However, 2-phase models provided more accurate 671 predictions of the budburst date for particular recent years with warm winter. This was 672 673 especially marked for Corvlus and Picea. Thus, a certain level of winter warming might have 674 been reached in the Alps, sometimes leading to non-optimal chilling conditions and later 675 dormancy release date compared to colder years. In such situation, the integration of an 676 endodormancy phase in the phenology model clearly increases the projections accuracy. The negative effect of winter warming on endodormancy release in tree species has been shown in 677 a previous study (Asse et al. 2018) and has also been proposed as an explanation of the 678 679 dampening of the response of budburst to warming temperature over the past 25 years in Europe (Fu et al., 2015). Although warm winter conditions are still rare in our past temperature records, they will become more frequent in the upcoming decades especially after 2050 according to climate projections. Such conditions are expected to delay dormancy release and ultimately delay or even prevent budburst (Fig. 2 & 4). In this context, it becomes essential and urgent that robust 2-phase models be available for as many tree species as possible.

Although chilling was taken into account in the correlative models, they did not project a negative effect of a lack of chilling on the budburst date like the 2-phase processbased model. Although the two types of models were calibrated with the same dataset which contained only one exceptionally warm winter (2006-2007) which had a delaying effect on the budburst date (Asse et al., 2018), it seems that only the process-based model was able to capture this important information.

692

693 *4.3. Evolution of the budburst date in the Alps over the 21st century*

694 At low elevation, projected budburst dates were similar until ca. 2050 for all models and for all species, with a weak linear trend towards earlier dates (Fig 5 & 6). This linear 695 696 trend is due to the warming of spring which accelerates cell elongation while the warming of 697 winter does not affect chilling accumulation until 2050 according to climate projections as previously highlighted by Vitasse et al., (2011); Chuine et al., (2016) and Fig. 1 in Guo et 698 699 al., (2015). However, after 2050, while the linear trend towards earlier dates continues and 700 accelerates in correlative and 1-phase models (although less in the latter and especially for 701 *Larix*), this trend progressively vanished in 2-phase models.

At high elevation, projected budburst dates were similar for all species over the 21st century between 1-phase and 2-phase models, suggesting that at high elevation, chilling requirements could be fulfilled until the end of the 21st century.

705 Thus, our results suggest that warmer winters might have opposite effects on spring 706 phenology at high compared to low elevation, by advancing vs delaying dormancy release 707 respectively, and consequently reducing the phenological cline across the elevation gradient. 708 As a consequence, trees might become at increasing risk of late spring frost damage at high 709 elevation compared to low elevation in the upcoming decades. A preview of such situations 710 have already been reported in the Swiss Alps over the last decades (Vitasse et al., 2017, 711 2018). Considering that phenological traits have been shown to be primary determinants of 712 species range (Chuine & Beaubien, 2001; Chuine et al., 2013), a reduced phenological shift 713 across the elevation gradient might in the medium term alter the altitudinal zonation of the 714 vegetation.

Our results also support the hypothesis of Vitasse *et al.*, (2017) that winter temperatures are currently actually colder than the optimal chilling temperature at high elevation so that a warming of winter actually increases the number of chilling days and advance endodormancy release, and consequently budburst. Bud endodormancy indeed requires from a few weeks to several months of cold temperature, that can vary from 0°C to 12°C depending on the species, to be fully released (Lang et al., 1987; Caffarra et al., 2011a; Malagi et al., 2015).

From 1950 to 2100, 2-phase models projected a trend for earlier budburst date in the inner Alps (higher elevations), while they projected either very weak trend toward earlier dates or a trend toward later dates in the outer Alps (lower elevations) (particularly for *Larix*

725 and Picea), and a trend toward later dates whatever the species in the Southern Alps, which 726 match or approach their southern range limit. In the short term, delaying effect of winter 727 warming on budburst date might be beneficial to trees by reducing the risk of exposure to late 728 spring frost. But in the longer term, it is expected to lead to partial dormancy release at low 729 elevation and at species southern range limit leading to leaf and flower malformation and 730 erratic bud break (Bonhomme et al., 2005; Erez, 2000; Petri & Leite, 2004; Zguigal et al., 2006; Caffarra et al., 2011b; Laube et al., 2014). Additionally to temperature, photoperiod 731 might also co-control budburst in about 30% of temperate tree species (Caffarra et al., 2011; 732 Basler and Körner, 2012; Laube et al., 2014; Zohner and Renner, 2015), with long 733 734 photoperiod compensating for a lack of chilling. Integration of this compensatory effect in the models might change substantially the projections of budburst dates for the end of the 21st 735 736 century for photosensitive species which might be the case for Picea abies (Blümel & Chmielewski, 2012; Gauzere et al., 2017). 737

738

739 *Conclusion*

740 Our results showed that (1) process-based phenology models are more robust than 741 correlative model even when they rely entirely on backward estimation (inverse modelling) 742 of their parameter values. (2) They also demonstrated that the robustness of process-based 743 models could be increased, though not substantially, when their calibration could rely on 744 forward estimation. Therefore, the robustness of process-based models seems to come 745 primarily from the explicit description of causal relationships rather than from forward estimation of model parameters, and we advise using, whenever possible, both backward and 746 forward estimation of model parameters. (3) In opposite to correlative models, process-based 747

748 models projected a reduction in the phenological cline along the elevation gradient for all 749 species by the end of the 21st century. This later result suggests that using linear relationships 750 to provide projections for the second part of the 21st century will be vain, especially at low 751 elevation and at species southern range limits.

752

753 Acknowledgements

754 We are grateful to all the volunteers and staffs of protected areas involved in the 755 Phenoclim program for their help and support for collecting data on the study sites. We also 756 thank Geoffrey Klein (Centre de Recherches sur les Ecosystèmes d'Altitude CREA, 757 Chamonix-Mont-Blanc) for having prepared the temperature data used in this study. We 758 thank the Conservatoire Botanique National Alpin for providing the species occurrence data, 759 and two anonymous referees for their constructive comments on earlier versions of the manuscript. This research project was funded by the Association Nationale de la Recherche et 760 761 de la Technologie (ANRT). This work is part of the project "Phenoclim" supported by the 762 Rhône-Alpes and PACA Regions, French ministry of Transition écologique et solidaire. We 763 thank the Société Académique Vaudoise (SAV) for having kindly provided matching funds.

764

766 **References**

- Anderson, J.J., Gurarie, E., Bracis, C., Burke, B.J., Laidre, K.L., 2013. Modeling climate
 change impacts on phenology and population dynamics of migratory marine species.
 Ecol. Modell. 264, 83–97. doi:10.1016/j.ecolmodel.2013.03.009
- 709 Ecol. Modell. 204, 85–97. dol:10.1016/j.ecolmodel.2015.05.009
- Asse, D., Chuine, I., Vitasse, Y., Yoccoz, N.G., Delpierre, N., Badeau, V., Delestrade, A.,
 Randin, C.F., 2018. Warmer winters reduce the advance of tree spring phenology
 induced by warmer springs in the Alps. Agric. For. Meteorol. 252, 220–230.
 doi:10.1016/j.agrformet.2018.01.030
- Basler, D., 2016. Evaluating phenological models for the prediction of leaf-out dates in six
 temperate tree species across central Europe. Agric. For. Meteorol. 217, 10–21.
 doi:10.1016/j.agrformet.2015.11.007
- Basler, D., Körner, C., 2012. Photoperiod sensitivity of bud burst in 14 temperate forest tree
 species. Agric. For. Meteorol. 165, 73–81. doi:10.1016/j.agrformet.2012.06.001
- Bellon-Maurel, V., Fernandez-Ahumada, E., Palagos, B., Roger, J.M., McBratney, A., 2010.
 Critical review of chemometric indicators commonly used for assessing the quality of
 the prediction of soil attributes by NIR spectroscopy. TrAC Trends Anal. Chem.
 doi:10.1016/j.trac.2010.05.006
- Benmoussa, H., Ben Mimoun, M., Ghrab, M., Luedeling, E., 2018. Climate change threatens
 central Tunisian nut orchards. Int. J. Biometeorol. 62, 2245–2255. doi:10.1007/s00484018-1628-x
- Blümel, K., Chmielewski, F.M., 2012. Shortcomings of classical phenological forcing models
 and a way to overcome them. Agric. For. Meteorol. 164, 10–19.
 doi:10.1016/j.agrformet.2012.05.001
- Bonhomme, M., Rageau, R., Lacointe, A., Gendraud, M., 2005. Influences of cold
 deprivation during dormancy on carbohydrate contents of vegetative and floral
 primordia and nearby structures of peach buds (Prunus persica L. Batch). Sci. Hortic.
 (Amsterdam). 105, 223–240. doi:10.1016/j.scienta.2005.01.015
- 793 Bray, D., Storch, H. Von, 2009. "Prediction" or "Projection"? 534–543.
- Burghardt, L.T., Metcalf, C.J.E., Wilczek, A.M., Schmitt, J., Donohue, K., 2015. Modeling
 the Influence of Genetic and Environmental Variation on the Expression of Plant Life
 Cycles across Landscapes. Am. Nat. 185, 212–227. doi:10.1086/679439
- Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference: a practical
 information-theoretic approach, Ecological Modelling.
 doi:10.1016/j.ecolmodel.2003.11.004
- Caffarra, A., Donnelly, A., Chuine, I., 2011a. Modelling the timing of Betula pubescens
 budburst. II. Integrating complex effects of photoperiod into process-based models.
 Clim. Res. 46, 159–170. doi:10.3354/cr00983
- Caffarra, A., Donnelly, A., Chuine, I., Jones, M.B., 2011b. Modelling the timing of Betula
 pubescens budburst. I. Temperature and photoperiod: A conceptual model. Clim. Res.
 46, 147–157. doi:10.3354/cr00980
- Cheaib, A., Badeau, V., Boe, J., Chuine, I., Delire, C., Dufrêne, E., François, C., Gritti, E.S.,
 Legay, M., Pagé, C., Thuiller, W., Viovy, N., Leadley, P., 2012. Climate change impacts
 on tree ranges: Model intercomparison facilitates understanding and quantification of
 uncertainty. Ecol. Lett. 15, 533–544. doi:10.1111/j.1461-0248.2012.01764.x
- 809 uncertainty. Ecol. Lett. 15, 533-544. doi:10.1111/j.1461-0248.2012.01/64.x
- Chuine, I., 2010. Why does phenology drive species distribution? Philos. Trans. R. Soc. B
 Biol. Sci. 365, 3149–3160. doi:10.1098/rstb.2010.0142
- 812 Chuine, I., 2000. A Unified Model for Budburst of Trees. J. Theor. Biol. 207, 337–347.

- 813 doi:10.1006/jtbi.2000.2178
- Chuine, I., Beaubien, E.G., 2001. Phenology is a major determinant of tree species range.
 Ecol. Lett. 4, 500–510. doi:10.1046/j.1461-0248.2001.00261.x
- Chuine, I., Bonhomme, M., Legave, J.M., Garcia de Cortazar-Atauri, I., Charrier, G.,
 Lacointe, A., Améglio, T., 2016. Can phenological models predict tree phenology
 accurately in the future? The unrevealed hurdle of endodormancy break. Glob. Chang.
 Biol. 22, 3444–3460. doi:10.1111/gcb.13383
- Chuine, I., Cour, P., Rousseau, D.D., 1999. Selecting models to predict the timing of
 flowering of temperate trees: Implications for tree phenology modelling. Plant, Cell
 Environ. 22, 1–13. doi:10.1046/j.1365-3040.1999.00395.x
- Chuine, I., Cour, P., Rousseau, D.D., 1998. Fitting models predicting dates of flowering of
 temperate-zone trees using simulated annealing. Plant, Cell Environ. 21, 455–466.
 doi:10.1046/j.1365-3040.1998.00299.x
- Chuine, I., De Cortazar-Atauri, I.G., Kramer, K., Hänninen, H., 2013. Plant development
 models, in: Phenology: An Integrative Environmental Science. pp. 275–293.
 doi:10.1007/978-94-007-6925-0 15
- Chuine, I., Régnière, J., 2017. Process-Based Models of Phenology for Plants and Animals.
 Annu. Rev. Ecol. Evol. Syst. 48, 159–182. doi:10.1146/annurev-ecolsys-110316-022706
- Cianfrani, C., Satizábal, H.F., Randin, C., 2015. A spatial modelling framework for assessing
 climate change impacts on freshwater ecosystems : Response of brown trout (Salmo
 trutta L .) biomass to warming water temperature. Ecol. Modell. 313, 1–12.
 doi:10.1016/j.ecolmodel.2015.06.023
- Cooke, J.E.K., Weih, M., 2005. Nitrogen storage and seasonal nitrogen cycling in Populus:
 Bridging molecular physiology and ecophysiology. New Phytol. doi:10.1111/j.14698137.2005.01451.x
- Bantec, C.F., Vitasse, Y., Bonhomme, M., Louvet, J.M., Kremer, A., Delzon, S., 2014.
 Chilling and heat requirements for leaf unfolding in European beech and sessile oak
 populations at the southern limit of their distribution range. Int. J. Biometeorol. 58,
 1853–1864. doi:10.1007/s00484-014-0787-7
- Delpierre, N., Soudani, K., François, C., Köstner, B., Pontailler, J.Y., Nikinmaa, E., Misson,
 L., Aubinet, M., Bernhofer, C., Granier, A., Grünwald, T., Heinesch, B., Longdoz, B.,
 Ourcival, J.M., Rambal, S., Vesala, T., Dufrêne, E., 2009. Exceptional carbon uptake in
 European forests during the warm spring of 2007: A data-model analysis. Glob. Chang.
 Biol. 15, 1455–1474. doi:10.1111/j.1365-2486.2008.01835.x
- Buputié, A., Rutschmann, A., Ronce, O., Chuine, I., 2015. Phenological plasticity will not
 help all species adapt to climate change. Glob. Chang. Biol. 21, 3062–3073.
 doi:10.1111/gcb.12914
- Erez, A., 2000. Bud Dormancy; Phenomenon, Problems and Solutions in the Tropics and
 Subtropics. Temp. Fruit Crop. Warm Clim. 17–48. doi:10.1007/978-94-017-3215-4_2
- Fu, Y.H., Piao, S., Op de Beeck, M., Cong, N., Zhao, H., Zhang, Y., Menzel, A., Janssens,
 I.A., 2014. Recent spring phenology shifts in western Central Europe based on
- multiscale observations. Glob. Ecol. Biogeogr. 23, 1255–1263. doi:10.1111/geb.12210
 Fu, Y.H., Zhao, H., Piao, S., Peaucelle, M., Peng, S., Zhou, G., Ciais, P., Song, Y., Vitasse,
- Y., Zeng, Z., Janssens, I. a, Huang, M., Menzel, A., Pen, J., 2015. Declining global
 warming effects on the phenology of spring leaf unfolding. Nature 526, 104–107.
 doi:10.1038/nature15402
- Gauzere, J., Delzon, S., Davi, H., Bonhomme, M., Garcia de Cortazar-Atauri, I., Chuine, I.,
 2017. Integrating interactive effects of chilling and photoperiod in phenological process-

- 861 based models. A case study with two European tree species: Fagus sylvatica and
- 862 Quercus petraea. Agric. For. Meteorol. 244–245, 9–20.
- 863 doi:10.1016/j.agrformet.2017.05.011
- Guo, L., Dai, J., Wang, M., Xu, J., Luedeling, E., 2015. Responses of spring phenology in
 temperate zone trees to climate warming: A case study of apricot flowering in China.
 Agric. For. Meteorol. 201, 1–7. doi:10.1016/j.agrformet.2014.10.016
- Hanninen, H., 1987. Effects of temperature on dormancy release in woody plants:
 implications of prevailing models. Silva Fenn.
- Higgins, S.I., O'Hara, R.B., Römermann, C., 2012. A niche for biology in species
 distribution models. J. Biogeogr. 39, 2091–2095. doi:10.1111/jbi.12029
- Hogg, E.H., Price, D.T., Black, T.A., 2000. Postulated feedbacks of deciduous forest
 phenology on seasonal climate patterns in the Western Canadian interior. J. Clim. 13,
 4229–4243. doi:10.1175/1520-0442(2000)013<4229:PFODFP>2.0.CO;2
- Howe, G.T., Saruul, P., Davis, J., Chen, T.H.H., 2000. Quantitative genetics of bud
 phenology, frost damage, and winter survival in an F 2 family of hybrid poplars. TAG
 Theor. Appl. Genet. 101, 632–642. doi:10.1007/s001220051525
- Janssen, P.H.M., Heuberger, P.S.C., 1995. Calibration of process-oriented models. Ecol.
 Modell. 83, 55–66. doi:10.1016/0304-3800(95)00084-9
- Jones, H.G., Hillis, R.M., Gordon, S.L., Brennan, R.M., 2013. An approach to the
 determination of winter chill requirements for different Ribes cultivars. Plant Biol. 15,
 18–27. doi:10.1111/j.1438-8677.2012.00590.x
- Kearney, M.R., Wintle, B.A., Porter, W.P., 2010. Correlative and mechanistic models of
 species distribution provide congruent forecasts under climate change. Conserv. Lett. 3,
 203–213. doi:10.1111/j.1755-263X.2010.00097.x
- Kollas, C., Randin, C.F., Vitasse, Y., Körner, C., 2014. Agricultural and Forest Meteorology
 How accurately can minimum temperatures at the cold limits of tree species be
 extrapolated from weather station data ? Agric. For. Meteorol. 184, 257–266.
 doi:10.1016/j.agrformet.2013.10.001
- Körner, C., 1999. Alpine plant life: functional plant ecology of high mountain ecosystems,
 Alpine plant life functional plant ecology of high mountain ecosystems.
 doi:10.1659/0276-4741(2001)021[0202:APLFPE]2.0.CO;2
- Lang, G., Early, J., Martin, G., Darnell, R., 1987. Endo-, para-, and ecodormancy:
 physiological terminology and classification for dormancy research. HortScience.
- Laube, J., Sparks, T.H., Estrella, N., Höfler, J., Ankerst, D.P., Menzel, A., 2014. Chilling
 outweighs photoperiod in preventing precocious spring development. Glob. Chang. Biol.
 20, 170, 182, doi:10.1111/coch.12260
- 896 20, 170–182. doi:10.1111/gcb.12360
- Lebourgeois, F., Pierrat, J.C., Perez, V., Piedallu, C., Cecchini, S., Ulrich, E., 2010.
 Simulating phenological shifts in French temperate forests under two climatic change
 scenarios and four driving global circulation models. Int. J. Biometeorol. 54, 563–581.
 doi:10.1007/s00484-010-0305-5
- Lindstrom, M., Bates, D., 1990. Nonlinear mixed effects models for repeated measures data.
 Biometrics. doi:10.2307/2532087
- Linkosalo, T., Lappalainen, H.K., Hari, P., 2008. A comparison of phenological models of
 leaf bud burst and flowering of boreal trees using independent observations. Tree
 Physiol. 28, 1873–1882. doi:10.1093/treephys/28.12.1873
- Lobell, D.B., Burke, M.B., 2010. On the use of statistical models to predict crop yield
 responses to climate change. Agric. For. Meteorol. 150, 1443–1452.
 doi:10.1016/j.acrformat.2010.07.008
- 908 doi:10.1016/j.agrformet.2010.07.008

- Luedeling, E., Zhang, M., McGranahan, G., Leslie, C., 2009. Validation of winter chill
 models using historic records of walnut phenology. Agric. For. Meteorol. 149, 1854–
 1864. doi:10.1016/j.agrformet.2009.06.013
- Malagi, G., Sachet, M.R., Citadin, I., Herter, F.G., Bonhomme, M., Regnard, J.L., Legave,
 J.M., 2015. The comparison of dormancy dynamics in apple trees grown under
 temperate and mild winter climates imposes a renewal of classical approaches. Trees Struct. Funct. 29, 1365–1380. doi:10.1007/s00468-015-1214-3
- 916 Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aaasa, A., Ahas, R., Alm-Kübler, K.,
- Bissolli, P., Braslavská, O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y.,
 Dahl, Å., Defila, C., Donnelly, A., Filella, Y., Jatczak, K., Måge, F., Mestre, A., Nordli,
 Ø., Peñuelas, J., Pirinen, P., Remišová, V., Scheifinger, H., Striz, M., Susnik, A., Van
 Vliet, A.J.H., Wielgolaski, F.E., Zach, S., Zust, A., 2006. European phenological
 response to climate change matches the warming pattern. Glob. Chang. Biol. 12, 1969–
 1976. doi:10.1111/j.1365-2486.2006.01193.x
- Morin, X., Thuiller, W., 2009. Comparing niche- and process-based models to reduce
 prediction uncertainty in species range shifts under climate change. Ecology 90, 1301–
 1313. doi:10.1890/08-0134.1
- Mountain Research Initiative EDW Working Group, 2015. Elevation-dependent warming in mountain regions of the world. Nat. Clim. Chang. 5, 424–430.
 doi:10.1038/nclimate2563\rhttp://www.nature.com/nclimate/journal/v5/n5/abs/nclimate
- 929 2563.html#supplementary-information
- Nagano, A.J., Sato, Y., Mihara, M., Antonio, B.A., Motoyama, R., Itoh, H., Nagamura, Y.,
 Izawa, T., 2012. Deciphering and prediction of transcriptome dynamics under
 fluctuating field conditions. Cell 151, 1358–1369. doi:10.1016/j.cell.2012.10.048
- Nash, J.E., Sutcliffe, J. V., 1970. River flow forecasting through conceptual models part I A
 discussion of principles. J. Hydrol. 10, 282–290. doi:10.1016/0022-1694(70)90255-6
- Nissanka, S.P., Karunaratne, A.S., Perera, R., Weerakoon, W.M.W., Thorburn, P.J., Wallach,
 D., 2015. Calibration of the phenology sub-model of APSIM-Oryza: Going beyond
- goodness of fit. Environ. Model. Softw. 70, 128–137. doi:10.1016/j.envsoft.2015.04.007
 Olesen, J.E., Trnka, M., Kersebaum, K.C., Skjelvåg, A.O., Seguin, B., Peltonen-Sainio, P.,
- Rossi, F., Kozyra, J., Micale, F., 2011. Impacts and adaptation of European crop
 production systems to climate change. Eur. J. Agron. 34, 96–112.
 doi:10.1016/j.eja.2010.11.003
- Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts
 across natural systems. Nature 421, 37–42. doi:10.1038/nature01286
- Petri, J.L., Leite, G.B., 2004. Consequences of insufficient winter chilling on apple tree bud break, in: Acta Horticulturae. pp. 53–60. doi:10.17660/ActaHortic.2004.662.4
- Pinheiro, J.C., Bates, D.M., 1996. Unconstrained parametrizations for variance-covariance
 matrices. Stat. Comput. 6, 289–296. doi:10.1007/BF00140873
- R Core Team, 2016. R: A language and environment for statistical computing. Version 3.3.2.
 R Found. Stat. Comput. Vienna, Austria. doi:10.1017/CBO9781107415324.004
- Randin, C.F., Dirnböck, T., Dullinger, S., Zimmermann, N.E., Zappa, M., Guisan, A., 2006.
 Are niche-based species distribution models transferable in space? J. Biogeogr. 33, 1689–1703. doi:10.1111/j.1365-2699.2006.01466.x
- Rebetez, M., Reinhard, M., 2008. Monthly air temperature trends in Switzerland 1901-2000
 and 1975-2004. Theor. Appl. Climatol. 91, 27–34. doi:10.1007/s00704-007-0296-2
- 955 Richardson, A.D., Anderson, R.S., Arain, M.A., Barr, A.G., Bohrer, G., Chen, G., Chen,
- 956 J.M., Ciais, P., Davis, K.J., Desai, A.R., Dietze, M.C., Dragoni, D., Garrity, S.R.,

- 957 Gough, C.M., Grant, R., Hollinger, D.Y., Margolis, H.A., Mccaughey, H., Migliavacca,
- 958 M., Monson, R.K., Munger, J.W., Poulter, B., Raczka, B.M., Ricciuto, D.M., Sahoo,
- A.K., Schaefer, K., Tian, H., Vargas, R., Verbeeck, H., Xiao, J., Xue, Y., 2012.
- 960 Terrestrial biosphere models need better representation of vegetation phenology: Results
 961 from the North American Carbon Program Site Synthesis. Glob. Chang. Biol. 18, 566–
 962 584 doi:10.1111/j.1265.2486.2011.02562 yr
- 962 584. doi:10.1111/j.1365-2486.2011.02562.x
- Satake, A., Kawagoe, T., Saburi, Y., Chiba, Y., Sakurai, G., Kudoh, H., 2013. Forecasting
 flowering phenology under climate warming by modelling the regulatory dynamics of
 flowering-time genes. Nat. Commun. 4. doi:10.1038/ncomms3303
- Schaber, J., Badeck, F.W., 2003. Physiology-based phenology models for forest tree species
 in Germany. Int. J. Biometeorol. 47, 193–201. doi:10.1007/s00484-003-0171-5
- Sen, P.K., 1968. Estimates of the Regression Coefficient Based on Kendall's Tau. J. Am.
 Stat. Assoc. 63, 1379–1389. doi:10.1080/01621459.1968.10480934
- Vitasse, Y., 2013. Ontogenic changes rather than difference in temperature cause understory
 trees to leaf out earlier. New Phytol. 198, 149–155. doi:10.1111/nph.12130
- Vitasse, Y., François, C., Delpierre, N., Dufrêne, E., Kremer, A., Chuine, I., Delzon, S., 2011.
 Assessing the effects of climate change on the phenology of European temperate trees.
 Agric. For. Meteorol. 151, 969–980. doi:10.1016/j.agrformet.2011.03.003
- Vitasse, Y., Rebetez, M., Filippa, G., Cremonese, E., Klein, G., Rixen, C., 2016. 'Hearing'
 alpine plants growing after snowmelt: ultrasonic snow sensors provide long-term series
- 977 of alpine plant phenology. Int. J. Biometeorol. 1–13. doi:10.1007/s00484-016-1216-x
 978 Vitasse, Y., Signarbieux, C., Fu, Y.H., 2017. Global warming leads to more uniform spring
 979 phenology across elevations. Proc. Natl. Acad. Sci. . doi:10.1073/pnas.1717342115
- Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin,
 J.M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate
 change. Nature 416, 389–395. doi:10.1038/416389a
- Wang, E., Engel, T., 1998. Simulation of phenological development of wheat crops. Agric.
 Syst. 58, 1–24. doi:10.1016/S0308-521X(98)00028-6
- 2guigal, A., Chahbar, A., Loudiyi, D.E.M.W., Crabbé, J., 2006. Caractéristiques de la
 dormance des bourgeons du pommier dans les régions à hiver doux. Biotechnol. Agron.
 Soc. Environ. 10, 131–137.
- Zohner, C.M., Benito, B.M., Svenning, J.C., Renner, S.S., 2016. Day length unlikely to
 constrain climate-driven shifts in leaf-out times of northern woody plants. Nat. Clim.
 Chang. 6, 1120–1123. doi:10.1038/nclimate3138
- Zohner, C.M., Renner, S.S., 2015. Perception of photoperiod in individual buds of mature
 trees regulates leaf-out. New Phytol. 208, 1023–1030. doi:10.1111/nph.13510
- Zohner, C.M., Renner, S.S., 2014. Common garden comparison of the leaf-out phenology of
 woody species from different native climates, combined with herbarium records,
- 995 forecasts long-term change. Ecol. Lett. 17, 1016–1025. doi:10.1111/ele.12308
- 996

- 997 Appendix A
- 998

999 Phenoclim protocol

Phenoclim is a citizen science program initiated in 2004 (www.phenoclim.org) by CREA
(Centre de Recherches sur les Ecosystèmes d'Altitude, Chamonix, France), which aims at
assessing the long-term effects of climate change on plant phenology over the French Alps.
The specificity of this program, compared to other existing citizen science initiatives, lies not
only in its large geographic coverage in mountain environments, but also in its simultaneous
acquisition of accurate temperature records in addition to phenological observations.

1006 In the Phenoclim protocol, budburst is defined as the first day at which 10% of vegetative 1007 buds of the crown on a given individual are opened (BBCH 07). At each site, observers 1008 survey at least two individuals per species. These individuals are chosen to be adult and 1009 dominant trees taller than 7 m, sharing similar environmental conditions (i.e. soil, slope and 1010 aspect) and at a maximum horizontal distance of 100 m from each other. Phenological observations were recorded weekly. For each species, yearly budburst dates were calculated 1011 as the mean date of individuals observed at a given site. The five surveyed species do not 1012 1013 occur simultaneously at all sites, therefore, the number of years surveyed varies for a given 1014 site (Fig.1). In total, and irrespective of species, 242 sites for budburst were surveyed 1015 between 2007 and 2014.

1016

1017

observation model. Var-j and chilling,	sites equipped with part= partitions of v two P values are p	h tem varian rovide	perature ce betw 3d, one	e station een gro for each	ns and on al wing degree effect.	ll observati >-days > 0°	ion sites. A C (GGD0)	djusted R-sq , growing deg	luared (R gree-days	²), AIC > 5°C (, and <i>P</i> . (GGD5)	-value of <i>F</i> , and chilli	ANOVA a ng. For me	re provide odels with	d for each both GDD
								Budb	ourst						
					With temper	ature station	JIS					All si	tes		
		Ν	AIC	\mathbb{R}^2	P-value (anova)	Var-part GDD0	Var-part chilling	Var-part - both	Z	AIC	\mathbb{R}^2	P-value (anova)	Var-part GDD0	Var-part chilling	Var-part - both
C. avellana		126							319						
	GDD0		929	0.55	* * *					2377	0.62	* *			
	GDD5		940	0.51	* *					2404	0.59	* *			
	Chilling		967	0.26	*					2502	0.38	* *			
	GDD0+Chilling		921	0.54	SN/***	0.30	0.01	0.11		2373	0.62	***/NS	0.28	0.0	0.18
E anodeiou	GDD3+Chilling	150	932	0.52	SN/***	0.24	10.0	0.12	200	2392	0.60	*** **	0.23	0.0	0.18
r. exceisior	UUUD	701	1137	0.65	****				060	07070	0.70	***			
	SUDS		1122	0.65	* *					2949 2058	0.70	* *			
	Chilling		1174	0.50	*					3106	0.53	* *			
			1176	790	01V/***		00			1011		SIN/***	0 73	00	0.32
	GDD5+Chilling		1127	0.65	SN/***	0.23	0.0	0.22		2953	0.70	SN/***	0.22	0.0	0.33
B. pendula		145							307						
	GDD0		1040	0.72	* * * * * *					2224	0.76	* * * * * *			
	Chilling		1120	0.54	*					7202	0.55	* *			
	Chutung CDD0+Chilling		1047		0IN/***	0.27	00	c c			7C.0	SIV/***	0.27	00	0 72
	GDD5+Chilling		1044	0.73	SN/***	0.35	0.0	0.3		2222	0.76	SN/***	0.33	0.0	0.23
L. decidua		155							303						
	GDD0		1113	0.68	* *					2174	0.74	* *			
	GDD5		1109	0.69	* *					2180	0.72	* *			
	Chilling		1179	0.42	*					2367	0.43	* *			
	GDD0+Chilling		1109	0.68	***/NS	0.29	0.0	0.12		2171	0.74	SN/***	0.36	0.0	0.13
	GDD5+Chilling		1105	0.69	***/NS	0.29	0.0	0.12		2176	0.72	***/NS	0.34	0.0	0.13
P. abies		107							248						
	GDD0		752	0.79	* *					1757	0.81	* *			
	GDD5		743	0.81	***					1738	0.84	* *			
	Chilling		833	0.44	*					1949	0.43	* *			
	GDD0+Chilling		745	0.78	SN/***	0.50	0.01	0.15		1752	0.81	sn/***	0.38	0.0	0.28
	GDD5+Chilling		733	0.81	*/***	0.54	0.02	0.14		1725	0.84	**/***	0.41	0.01	0.27

Appendix B Linear mixed models of budburst dates as response variables and temperature-based factors as competing predicting variables. Models are calibrated both on

Appendix C

Parameter estimates obtained for each model when calibrated on observation sites with weather stations and performances indices. *N*: number of observations; *k*: number of parameters. N number of data; k number of parameters; SStot total variance (sum of squares), SSres residual variance (sum of squares); RMSE Root mean squared error; EFF efficiency; AICc Corrected Akaike's Information Criteria.

			1-phase mo	del	2-phase	model
с · -					Threshold	
Species	2	GDD	Sigmoïd	Wang	lower/sigmoïd	Wang/sigmoïd
C. avellana	Parameters	$t_0 = 1$	$t_0 = 57$	$t_0 = 51$	$t_0 = -115$	$t_0 = -119$
		F = 21	F = 8	F = 6	C = 145	C = 150
		$T_{b} = 7.12$	$d_{\rm T} = -0.45$	$T_{opt} = 27.95$	F = 11	F = 4
			$T_{50} = 8.44$	$T_{min} = -2.94$	$T_{\rm h} = 16$	$T_{opt} = 5.0^{7}$
				$T_{max} = 41.13$	$d_{\rm T} = -0.38$	$T_{min} = -4.47$
					$1_{50} = 8.61$	$I_{max} = 22.07$
						$d_{\rm T} = -1./1$ T = 7.01
	Calibration performances					$1_{50} - 7.91$
	N	128	128	128	128	128
	k	3	4	5	6	8
	SStot	22262	19743	19743	19743	19743
	SSres	16559	9815	9796	8564	7470
	RMSF	10.91	8 76	8 75	8 18	7 64
	FFF	0.26	0.5	0.5	0.57	0.62
	AICc	626 51	563.80	565 72	550.72	537.74
	nice	020.51	505.00	505.72	550.72	
F. excelsior	Parameters	$t_0 = 1$	$t_0 = 54.7$	$t_0 = 55$	$t_0 = -77$	$t_0 = -78$
		F = 121	F = 17	F = 23	C = 125	C =125
		$T_{b} = 5.68$	$d_{\rm T} = -0.22$	$T_{opt} = 16.2$	F' = 9	F' = 9
			$T_{50} = 12.25$	$T_{min} = -38.8$	$T_{\rm h} = 10.6$	$T_{opt} = 0.1$
				$T_{max} = 20.8$	$d_{\rm T} = -0.2$	$T_{min} = -36.6$
					$T_{50} = 16.2$	$T_{max} = 21.3$
						$d_{\rm T} = -0.24$
	Caliburgian and announces					$T_{50} = 10.41$
	Calibration performances	140	140	140	140	1.40
	IN 1-	149	149	149	149	149
	K	3	4	5	0	8
	55101	34545	312/5	312/5	312/5	312/5
	SSres	19787	12559	12650	11958	12430
	RMSE	10.98	9.22	9.21	8.96	9.13
	EFF	0.43	0.59	0.60	0.62	0.60
	AICc	732.52	670.37	672.20	665.98	676.19
B. pendula	Parameters	$t_0 = 1$	$t_0 = 60$	$t_0 = 62$	$t_0 = -101$	$t_0 = -108$
_ · <i>p</i> · · · · ·		$F^* = 72$	$F^* = 1$	$F^* = 9$	$C^* = 127$	$C^* = 157$
		$T_{\rm h} = 4.9$	$d_{\rm T} = -0.2$	$T_{res} = 17.4$	$F^* = 5$	$F^* = 5$
		-0,	$T_{50} = 24.5$	$T_{min} = -37.5$	$T_{\rm b} = 12.2$	$T_{res} = 3.4$
			150 21.5	$T_{min} = 21.5$	$d_{\rm r} = -0.2$	$T_{opt} = -9.9$
				1 max 21.0	$T_{50} = 16.97$	$T_{min} = 26.2$
					150 10.97	$d_{\rm max} = -0.2$
						$T_{ro} = 14.7$
	Calibration performances					150 14.7
	N	146	146	146	146	146
	k	3	4	5	6	8
	SStot	30844	30313	30313	30313	30313
	SSres	14743	8425	8440	8298	7720
	RMSE	9.69	7.6	7.6	7.5	7 27
	FFF	0.52	0.72	0.72	0.73	0.75
	AICc	677.86	600.36	601.89	602.46	596 38
	11100	077.00	000.00	001.07	002.40	570.50

			1-phase mo	del	2-phase	model
					Threshold	
Species		GDD	Sigmoïd	Wang	lower/sigmoïd	Wang/sigmoïd
L. decidua	Parameters	$t_0 = 1$	$t_0 = 83$	$t_0 = 83$	$t_0 = -100.8$	$t_0 = 66$
		$F^{*} = 3$	$F^* = 6$	$F^* = 6$	$C^* = 184$	$C^* = 134$
		$T_{b} = 9.6$	$d_{\rm T} = -37$	$T_{opt} = 10.1$	$F^* = 6$	$F^* = 6$
			$T_{50} = 6.2$	$T_{min} = 5.9$	$T_{h} = 18.3$	$T_{opt} = 9$
				$T_{max} = 37.7$	$d_{\rm T} = -37.4$	$T_{min} = -38.9$
					$T_{50} = 6.2$	$T_{max} = 34.2$
						$d_{\rm T} = -7.1$
						$T_{50} = 6.2$
	Calibration performances					
	Ν	159	159	159	159	159
	k	3	4	5	6	8
	SStot	27728	26275	26275	26275	26275
	SSres	54044	11328	11240	11297	10911
	RMSE	17.83	8.44	8.41	8.43	8.28
	EFF	-0.95	0.57	0.57	0.57	0.58
	AICc	930.83	686.58	687.47	690.43	689.31
D. 1.						
P. abies	Parameters	$t_0 = 1$	$t_0 = 83$	$t_0 = 84$	$t_0 = -100$	$t_0 = -107$
		F = 290	F = 5	F' = 8	C' = 174	C = 176
		$T_{b} = 2.96$	$d_{\rm T} = -0.1$	$T_{opt} = 29.9$	F' = 8	F' = 3
			$T_{50} = 24.2$	$T_{min} = -36.3$	$T_{\rm h} = 13.9$	$T_{opt} = 0.01$
				$T_{max} = 37.6$	$d_{\rm T} = -0.2$	$T_{min} = -39.8$
					$T_{50} = 18.1$	$T_{max} = 24.9$
						$d_{\rm T} = -0.2$
	~					$T_{50} = 27.6$
	Calibration performances					
	Ν	112	112	112	112	112
	k	3	4	5	6	8
	SStot	22158	21453	21453	21453	21453
	SSres	10623	4989	4984	4660	4753
	RMSE	9.29	6.67	6.67	6.45	6.51
	EFF	0.52	0.77	0.77	0.78	0.78
	AICc	513.97	433.58	435.66	430.36	437.18

Appendix D

Model performance in predicting the budburst date in the calibration conditions. Meteo sites refers to observation sites with meteorological stations; West sites refers Correlative 1 refers to the linear mixed model with GDD only. Correlative 2 refers to the linear model with GDD and chilling as variables. PB 1-phase uses a sigmoid function of temperature for the ecodormancy phase. PB 2-phase uses a lower threshold function of temperature for the endodormancy phase and a sigmoid function of temperature for the ecodormancy phase. PB calibrated refers to the 2-phase model which parameter estimates have been derived from experimental results. AICc, corrected Akaike criterion; EFF, model efficiency; RMSE, roots-mean-squared error (days); RMSEs, systematic root mean square error (days); RPIQ, to observations sites West of the species-specific longitudinal threshold; East sites refers to observation sites East of the species-specific longitudinal threshold. ratio of performance to interquartile distance; N, number of data used to fit the model.

Calibration sites			Meter	o sites					West	sites					East	sites		
	AICc	EFF	RMSE	RMSEs	RPIQ	N	AICc	EFF	RMSE	RMSEs	RPIQ	Z	AICc	EFF	RMSE	RMSEs	RPIQ	Ν
Betula																		
Correlative 1	964.1	0.79	6.62	6.58	2.87	145	1036.9	0.87	6.23	6.19	3.61	159	974.4	0.72	6.45	6.37	2.48	148
Correlative 2	964.1	0.80	6.62	6.58	2.87	145	1037.0	0.87	6.23	6.19	3.61	159	969.8	0.73	6.35	6.27	2.52	148
PB 1-phase	7.999	0.74	7.46	7.44	2.55	145	1180.1	0.68	9.72	9.71	2.32	159	1004.2	0.66	7.07	7.05	2.26	148
PB 2-phase	995.4	0.75	7.36	7.33	2.58	145	1173.1	0.70	9.53	9.49	2.36	159	1003.8	0.66	7.06	7.04	2.27	148
Corylus																		
Correlative 1	882.5	0.59	7.89	7.83	1.94	126	1067.8	0.70	7.69	7.60	2.47	154	1149.1	0.68	7.81	7.72	2.18	165
Correlative 2	879.9	0.60	7.81	7.75	1.99	126	1064.0	0.71	7.60	7.51	2.50	154	1148.8	0.68	7.81	7.72	2.18	165
PB 1-phase	902.2	0.51	8.58	8.47	1.81	126	1141.0	0.52	9.80	9.64	1.94	154	1219.0	0.52	9.58	9.55	1.77	165
PB 2-phase	886	0.58	7.98	7.94	1.94	126	1129.8	0.57	9.31	9.29	2.04	154	1212.2	0.55	9.37	9.35	1.81	165
Fraxinus																		
Correlative 1	1047.7	0.73	7.5	7.44	2.56	152	1129.8	0.82	6.55	6.47	3.36	171	1300.2	0.75	8.22	8.14	2.80	184
Correlative 2	1045.9	0.73	7.46	7.4	2.57	152	1134.6	0.82	6.63	6.56	3.32	171	1299.2	0.75	8.20	8.12	2.81	184
PB 1-phase	1137.7	0.51	10.12	10	1.90	152	1281.1	0.42	11.83	10.06	1.86	171	1366.8	0.49	11.66	9.76	1.97	184
PB 2-phase	1130	0.54	9.82	9.76	1.96	152	1280.6	0.41	11.88	10.05	1.85	171	1379.5	0.46	11.98	10.10	1.92	184
Larix																		
Correlative 1	1016.3	0.74	6.48	6.43	2.78	154	923.2	0.77	5.89	5.84	2.93	144	1055.1	0.80	6.75	69.9	3.07	158
Correlative 2	1016.1	0.74	6.47	6.42	2.78	154	921.0	0.77	5.85	5.80	2.95	144	1056.6	0.80	6.78	6.72	3.06	158
PB 1-phase	1088.4	0.58	8.16	8.12	2.20	154	1019.3	0.56	8.16	8.16	2.11	144	1109.4	0.72	8.00	7.94	2.59	158
PB 2-phase	1088.1	0.59	8.15	8.12	2.21	154	1018.4	0.56	8.15	8.13	2.12	144	1105.5	0.73	7.90	7.85	2.63	158
PB calibrated	1127.5	0.38	9.95	9.22	1.81	154	1042.7	0.39	9.57	8.85	1.80	144	1149.3	0.65	9.04	9.01	2.30	158
Picea																		
Correlative 1	684.7	0.83	5.79	5.76	2.77	107	788.5	0.83	5.69	5.67	3.86	124	777.3	0.87	5.47	5.42	3.66	124
Correlative 2	681.4	0.83	5.7	5.68	2.81	107	785.3	0.86	5.62	5.60	3.92	124	768.5	0.88	5.27	5.23	3.79	124
PB 1-phase	702	0.8	6.29	6.25	2.54	107	837.6	0.78	6.93	6.91	3.17	124	894.6	0.68	8.71	8.70	2.29	124
PB 2-phase	695.6	0.82	6.08	6.06	2.63	107	831.2	0.79	6.76	6.74	3.25	124	890.7	0.69	8.57	8.57	2.33	124

Appendix E

Model performance in projecting the budburst date in external conditions. Model and site labels as in appendix D. No meteo sites 1 refers to observation sites without meteorological stations. R^2 , adjusted R-squared; RMSE, roots-mean-squared error (days); RMSEs, systematic root mean square error (days); Diff. RMSE, difference between RMSE of the calibration (shown in appendix D) and RMSE of the projection; RPIQ, ratio of performance to interquartile distance; N, number of data used to fit the model.

Calibration sites			Meteo s	stations					West :	sites					East s	sites		
Projection sites			No mete	o station					East s	sites					West	sites		
	\mathbb{R}^2	RMSE	RMSEs	RPIQ	Diff RMSE	z	\mathbb{R}^2	RMSE	RMSEs	RPIQ	Diff RMSE	z	\mathbb{R}^2	RMSE	RMSEs	RPIQ	Diff RMSE	z
Betula																		
Correlative 1	0.46	11.23	10.70	1.73	4.24	194	0.47	10.49	10.03	1.82	2.55	165	0.44	10.82	10.57	1.86	5.63	154
Correlative 2	0.44	11.44	10.94	1.73	4.24	193	0.47	10.60	10.05	1.82	2.56	165	0.44	10.81	10.56	1.85	5.81	154
PB 1-phase	0.50	10.45	10.32	1.85	2.70	193	0.47	10.51	10.12	1.93	-1.42	165	0.52	9.97	9.81	2.32	2.65	154
PB 2-phase	0.51	10.46	10.25	1.75	3.33	193	0.42	11.09	10.48	1.86	-0.91	165	0.57	9.31	9.30	2.36	2.46	154
Corylus																		
Correlative 1	0.61	10.90	10.33	1.60	3.34	244	0.61	10.98	10.01	1.62	2.80	199	0.53	10.91	10.68	1.76	3.01	197
Correlative 2	0.60	11.03	10.42	1.57	3.63	244	0.60	10.91	10.08	1.60	3.00	199	0.53	10.93	10.71	1.76	3.00	197
PB 1-phase	0.58	10.66	10.62	1.72	1.87	244	0.64	10.37	9.54	1.62	0.71	199	0.53	12.89	10.73	1.91	0.39	197
PB 2-phase	0.59	10.77	10.59	1.72	2.48	244	0.60	11.78	10.10	1.53	1.78	199	0.53	11.36	10.75	2.04	-0.06	197
Fraxinus																		
Correlative 1	0.48	10.86	10.19	2.13	3.40	162	0.50	8.78	8.53	2.09	4.43	148	0.56	12.08	11.47	2.11	2.69	159
Correlative 2	0.48	10.86	10.19	2.11	3.57	162	0.50	8.79	8.53	2.11	4.28	148	0.56	12.16	11.50	2.10	2.73	159
PB 1-phase	0.53	10.16	9.70	2.18	0.54	162	0.62	8.30	7.44	2.22	-1.46	148	0.68	9.72	9.68	1.78	1.23	159
PB 2-phase	0.55	10.69	9.55	2.16	0.95	162	0.56	8.62	8.03	1.95	-0.10	148	0.70	9.52	9.48	2.03	-0.62	159
Larix																		
Correlative 1	0.55	10.66	10.05	1.74	4.18	148	0.54	11.07	10.31	1.87	5.18	158	0.40	9.85	9.49	1.75	3.10	144
Correlative 2	0.55	10.69	10.09	1.73	4.22	148	0.52	10.05	10.55	1.85	4.20	158	0.40	10.00	9.52	1.72	3.22	144
PB 1-phase	0.62	9.28	9.21	1.99	1.12	148	0.69	8.77	8.41	2.37	0.61	158	0.55	8.18	8.18	2.11	0.18	144
PB 2-phase	0.62	9.26	9.21	1.99	1.11	148	0.69	8.75	8.40	2.37	0.60	158	0.56	8.15	8.14	2.12	0.25	144
PB calibrated	0.67	8.68	8.64	2.13	-1.27	148	0.64	9.14	9.12	2.27	-0.43	158	0.48	9.57	8.85	1.80	0.53	144
Picea																		
Correlative 1	0.66	9.01	8.81	2.44	3.22	140	0.66	9.29	8.91	2.15	3.60	124	0.72	8.87	7.86	2.48	3.40	124
Correlative 2	0.66	9.01	8.80	2.44	3.31	140	0.67	9.23	8.85	2.17	3.61	124	0.73	8.47	7.72	2.60	3.20	124
PB 1-phase	0.65	9.10	8.98	2.41	2.81	140	0.68	9.16	8.69	2.18	2.23	124	0.77	7.61	7.05	2.89	-1.10	124
PB 2-phase	0.63	9.63	9.27	2.28	3.55	140	0.69	8.70	8.69	2.30	1.94	124	0.79	6.75	6.73	3.26	-1.82	124

Appendix F

Comparison of predicted (a, c, e, g, i) and projected (b, d, f, h, j) budburst dates either by the correlative model (with GDD and chilling as variables) (blue dots) or the process-based 2-phase model (red dots) with observed budburst dates for each species. Linear regressions of predicted/projected dates on observed dates (superimposed lines) are shown for correlative model (blue) and process 2-phase model (red). Light grey area= \pm .95 confidence interval of dates predicted/projected by the correlative model. Dark grey area= \pm .95 confidence interval of dates predicted/projected by the 2-phase model.



Appendix G

Comparison of predicted (a, c, e, g, i) and projected (b, d, f, h, j) budburst dates either by the process 1-phase model (grey dots) or the process 2-phase model (red dots) with observed budburst dates for each species. Linear regression of predicted/projected budburst dates on observed dates (superimposed lines) are shown for process 1-phase model (grey) and process 2-phase model (red). Light grey area= \pm .95 confidence interval of dates predicted/projected by the 1-phase model. Dark grey area= \pm .95 confidence interval of dates predicted/projected by the 2-phase model.



Appendix H

Variation of the residuals of correlative models (with GDD and chilling as variables) (blue dots) and process-based 2-phase models (red dots) calculated either with the calibration data subset1 (a, c, e, g, i) or the validation data subset 2 (b, d, f, h, j) along the elevation gradient. Superimposed lines are linear regression of residuals on elevation (same color as symbols).



Appendix I

Variation of the residuals of process-based 1-phase models (grey dots) and process-based 2-phase models (red dots) calculated either with the calibration data subset1 (a, c, e, g, i) or the validation data subset 2 (b, d, f, h, j) along the elevation gradient. Superimposed lines are linear regression of residuals on elevation (same color as symbols).



Appendix J

Evolution and uncertainties of the climatic data generated by the ALADIN-Climat v5 RCM model (CNRM) for the CMIP5 experiment at a 12-km resolution, downscaled at 8-km resolution using quantile-quantile method (<u>http://drias-climat.fr/</u>). Daily minimum and maximum temperatures of RPC8.5 scenarios were extracted on the grid points of a rectangle area covering French Alps (43°48'N to 46°47'N, 5°59'E to 7°09'E). Black curve indicate the mean of annual mean temperature over the region (a), the mean of the annual average minimum temperature over the region (b), the mean of annual average maximum temperature over the region (d), and dark grey areas indicate the standard deviation.



Appendix K

elevation. Trend values indicate the Sen's slope per year and trendp values indicate the Sen's slope over the time period. Future climate data are according to scenario RCP8.5, in the Alps. Model labels as in appendix D. The elevation limits depend on species (Fig. 1 for elevation ranges). Mean annual shift of the budburst date projected over the periods 1950-2100, 1950-2050 and 2050-2100 in the French Alps at low elevation and high

				Low ele	ation				and an	High ele	evation		
Species	Model	1950-2	2100	1950	2050	2050-	.2100	1950-	-2100	1950.	-2050	2050-	2100
		trend	trendp	trend	trendp	trend	trendp	trend	trendp	trend	trendp	trend	trendp
C. avellana	Correlative Process-hased 1_nhase	-0.13	-22.90	-0.08	-7.50	-0.27	-13.90 -8 70	-0.08	-12.00	-0.03	-3.20 -16.80	-0.20	-10.40 -18.50
	Process-based 2-phase	-0.02	-2.50	-0.05	-4.60	0.08	3.90	-0.23	-34.40	-0.17	-16.50	-0.29	-14.50
F. excelsior	Correlative	-0.16	-24.30	-0.10	-10.10	-0.27	-13.80	-0.12	-17.70	-0.07	-6.60	-0.25	-12.60
	Process-based 1-phase Process-based 2-phase	-0.16 -0.05	-23.10 -7.90	-0.12	-11.30 -6.80	-0.20 0.020	-10.00 0.80	-0.23	-34.60 -31.80	-0.16 -0.16	-15.30	-0.32	-16.20 -13.60
B. pendula	Correlative Process-based 1-phase Process-based 2-phase	-0.25 -0.14	-37.70 -20.10 -5.70	-0.15 -0.10	-14.60 -9.50 -4.60	-0.45 -0.19 -0.01	-23.10 -9.40 -0.50	-0.10 -0.23 -0.22	-15.20 -34.00 -32.60	-0.05 -0.16	-4.50 -15.50 -15.60	-0.28 -0.33 -0.28	-14.50 -16.50 -13.80
L. decidua	Correlative Correlative Process-based 1-phase Forward calibrated PB	-0.24 -0.09 -0.02	-35.70 -13.00 -3.30 -8.10	-0.13 -0.09 -0.07 -0.01	-13.10 -9.30 -7.10 -1.10	-0.47 -0.03 0.16 -0.02	-24.20 -1.30 8.20 -1.10	-0.02 -0.31 -0.31 -0.29	-3.60 -46.20 -46.60 -43.40	-0.01 -0.20 -0.21 -0.20	-0.50 -19.70 -20.10 -19.60	-0.13 -0.42 -0.41 -0.38	-6.90 -20.90 -20.80 -19.10
P. abies	Correlative Process-based 1-phase Process-based 2-phase	-0.27 -0.14 -0.03	-40.60 -21.20 -3.80	-0.16 -0.11 -0.05	-16.30 -11.10 -5.30	-0.48 -0.19 0.10	-24.40 -9.70 5.10	-0.08 -0.25 -0.26	-12.70 -37.30 -38.80	-0.03 -0.17 -0.18	-3.00 -17.00 -18.00	-0.25 -0.32 -0.32	-12.80 -16.00 -15.80

Appendix L

Comparison of the budburst dates of *Larix decidua* predicted (a) and projected (b) by the processbased 2-phase model (red dots) and the forward calibrated process-based 2-phase model (brown dots) with the observed budburst dates. Linear regression of predicted/projected budburst dates on observed dates (superimposed lines) are shown for the 2-phase model (red) and the 2-phase calibrated model (brown). Red area= \pm .95 confidence interval of dates predicted/projected by the 2-phase model. Orange area= \pm .95 confidence interval of dates predicted/projected by the calibrated 2-phase model.



Appendix M

Variation of the residuals of process-based 2-phase models (red dots) and forward calibrated processbased 2-phase models (brown dots) calculated either with the calibration data subset1 (a, c, e, g, i) or the validation data subset 2 (b, d, f, h, j) along the elevation gradient. Superimposed lines are linear regression of residuals on elevation (same color as symbols).



Declaration of interests

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

- The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: