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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**

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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
37 why. In addition, the efficiency and robustness of the two model categories have rarely been
38 compared.

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

44 Process-based models were less efficient, yet more robust than correlative models,
45 even when their parameter estimates relied entirely on inverse modeling, i.e. parameter
46 values estimated using observed budburst dates and optimization algorithms. Their
47 robustness further slightly increased when their parameter estimates relied on forward
48 estimation, i.e. parameter values measured experimentally. Our results therefore suggest that
49 the robustness of process-based models comes both from the fact that they describe causal
50 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

53 effect of winter warming at low elevation where conditions will move away from optimal
54 chilling conditions that break bud dormancy vs an advancing effect of spring warming at high
55 elevation where optimal chilling conditions for dormancy release will persist even under the
56 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

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

64

65

66 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 yield (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 nutrient 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
85 of temperature (Howe *et al.*, 2000). This particular physiological state, called endodormancy
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

89 unfolding to warming after 2000. Ultimately, this lack of chilling temperatures might
90 compromise budburst itself at some point if warming continues (Chuine et al., 2016). Such a
91 situation is more likely to occur in populations inhabiting the warm edge of a species range
92 and/or lower elevations in mountain regions, where species are already in suboptimal chilling
93 conditions (Benmoussa et al., 2018; Guo et al., 2015). More than ever there is a need for
94 more accurate projections of tree phenology for the upcoming decades to remove the large
95 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,
117 2016). Another category of models, called 2-phase models, describes additionally the
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; Güzere *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*
130 *al.*, 2016), long photoperiod might compensate for insufficient chilling (Caffarra *et al.*,
131 2011a; Güzere *et al.* 2017).

132 There is now a large number of phenology models that differ in their level of
133 complexity and in the types of response function to environmental cues they use (see for
134 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
141 (Janssen and Heuberger, 1995); and by robustness, we mean here the ability of the model to
142 provide accurate predictions in external conditions (Janssen and Heuberger, 1995), i.e. other
143 conditions than those used to calibrate the model. Model's robustness determines its
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
148 relationship, sometimes involving other drivers as well (interaction between drivers). For this
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.

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

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

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

170 The Western Alps are particularly interesting to evaluate phenology models because
171 the elevation gradient provides a wide temperature range on a very short distance. In addition,
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
175 already increased in the Western Alps twice as fast as in the northern hemisphere during the
176 20th century (Rebetez and Reinhard, 2008) and recent evidence indicates that the current
177 warming rate increases with increasing elevation (Mountain Research Initiative EDW
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 non-

180 linear along elevation gradients. Therefore, ultimately, we aimed at answering a fourth
181 question: (4) How will climate change alter the budburst date of alpine species?

182

183 2. Methods

184 2.1. Phenological and meteorological data

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

195 Sixty of the observation sites (ranging from 372 to 1919 m a.s.l.) were equipped with
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
198 Semiconductor MAXIM, "<http://www.maxime-ic.com>", operating range of –55 to 125 °C
199 and an accuracy of 0.5 °C over the range of –10 to 85 °C) (Fig. 1). These data were used to
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
203 function of elevation. Residuals of this linear model were then interpolated using the
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*

207 realized at INRA UMR PIAF (Clermont-Ferrand, France) during winter 2010-2011. The aim
208 of this experiment was to determine the date of endodormancy release, the chilling required
209 to break endodormancy and the response of bud growth to temperature during the
210 ecodormancy phase of *Larix decidua* Mill. In a first experiment, 60 twigs of 30 to 40 cm,
211 were sampled on 4 sites (Saulzet, Orcival, Lamartine, Laqueuille) on February 2nd and
212 immediately taken to the laboratory. Twigs were recut under water and put in flasks filled up
213 with water. Water was subsequently changed twice a week. Twigs were divided into six sub-
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 $\mu\text{E}/\text{m}^2/\text{s}$, relative humidity (RH)
216 of 70%, except for the 5°C and 2°C chambers which received 20 $\mu\text{E}/\text{m}^2/\text{s}$ 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
221 recut under water and put in flasks filled up with water. Water was subsequently changed
222 twice a week. Twigs were placed in growth chambers (Sanyo MLR 351H) at 20°C, 16h
223 photoperiod, 50 $\mu\text{E}/\text{m}^2/\text{s}$, 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

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

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

244

245 2.3. Process-based phenology models

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

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

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

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

253 We used several versions of the model that differed by the response function to
254 temperature (R_f), which determines the daily rate of bud development:

255 the Growing Degree Day function, similarly to the correlative models,

$$256 R_f(T_d) = \text{Max}(0; T_d - T_b) \quad (2)$$

257 with T_b the lower threshold temperature;

258 and two more complex functions: the sigmoid function,

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

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

260 and the Wang function (Wang and Engel, 1998)

$$261 R_f = \text{Max} \left[\left(2(T_d - T_{min})^\alpha (T_{opt} - T_{min})^\alpha - \frac{(T_d - T_{min})^{2\alpha}}{(T_{opt} - T_{min})^{2\alpha}} \right), 0 \right] \quad (4)$$

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.

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

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

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

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

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

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

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

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

278 For the ecodormancy phase we used the best R_f function found with the 1-phase model for
 279 each species. These 2-phase models have 6 to 8 parameters that were either calibrated using
 280 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
 288 longitude corresponded to the longitude on both sides of which the species was equally
 289 present (i.e. 50% of the observation sites West of the longitude and 50% East of the
 290 longitude). The data subsets contained a similar number of data ($\bar{\sigma}=12$).

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

296 Correlative phenology models which corresponded to mixed effects models were
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.

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

310 Finally, we also used the experimental observations on *Larix* to constrain the
311 calibration of the best 2-phase model. Using the results of the two experiments, we were able
312 to estimate the critical sum of chilling during the endodormancy phase (C^*), the response
313 function to temperature (R_f) and the critical value F^* of the ecodormancy phase. We thus
314 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

318 Models were compared using four performance indices: adjusted R-square, Akaike’s
319 Information Criterion corrected for small sample size (AIC_C) (Burnham and Anderson,
320 2002); the efficiency (EFF) (Nash and Sutcliffe, 1970) ; the root mean square error for the
321 calibration (RMSE) and validation (RMSE_p) data sets respectively, the systematic root mean
322 square error (RMSEs) that estimates the model linear error (or bias).

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

323

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

324

$$RMSE_p \text{ or } RMSE = \sqrt{\frac{\sum_{i=1}^n (O_i - P_i)^2}{n}} \quad (10)$$

326

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

327 where O_i represents observed dates, P_i represents projected dates, \hat{P}_i represents regressed
328 prediction dates and N or n is the number of observations and k is the number of parameters.
329 We also used the ratio of performance to interquartile distance (RPIQ) that takes both the
330 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.

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

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

335 Based on the AICc, EFF, RMSE, RMSEs, RPIQ and R^2 (adjusted R-squared), we first
336 selected the best correlative model with GDD as variable, the best correlative model with
337 GDD and chilling as variables, and the best 1-phase and 2-phase models. We additionally
338 bootstrapped the best models (with 999 repetitions) to assess the effect of sampling bias on
339 RMSE indices, a good overall measure of model performance. We then calibrated linear
340 regressions of the model residuals (observed dates – predicted dates) as a function of
341 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
350 ecodormancy. To identify the three climatically contrasted years, we compared quantile
351 values of chilling and GDD between years for each species calculated as defined above.

352

353 *2.6. Model projections*

354 Following Bray & Storch (2009), we use the term “prediction” to refer to outputs of
355 models corresponding to the conditions used for the calibration; and the term ”projection” to
356 refer to outputs of models corresponding to conditions not used for the calibration. The term
357 “prediction” conveys a sense of certainty, while the term “projection” conveys a sense of
358 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
364 without meteorological stations (data subset2) using interpolated 2-m temperature for the
365 2007-2014 time period (see section 2.1). Second, we used models calibrated on observation
366 sites West of the species-specific longitude (data subset 3) to project the budburst date on
367 observation sites East of this longitude (data subset 4), and *vice versa*. The evaluation of the
368 models’ performance with data subsets 3 and 4 provides a more robust estimation of their
369 transferability compared to data subsets 1 and 2 because of the lower auto-correlation of the
370 meteorological conditions between them.

371 The accuracy of the projections was estimated using $RMSE_P$, $RMSE_S$, RPIQ and R^2 .
372 We additionally bootstrapped models (with 999 repetitions) to assess the effect of sampling
373 bias on RMSE indices. We finally calibrated linear regressions of the model residuals
374 (observed dates – projected dates) as a function of elevation.

375

376 *2.6.2. Projections across time using climate scenarios*

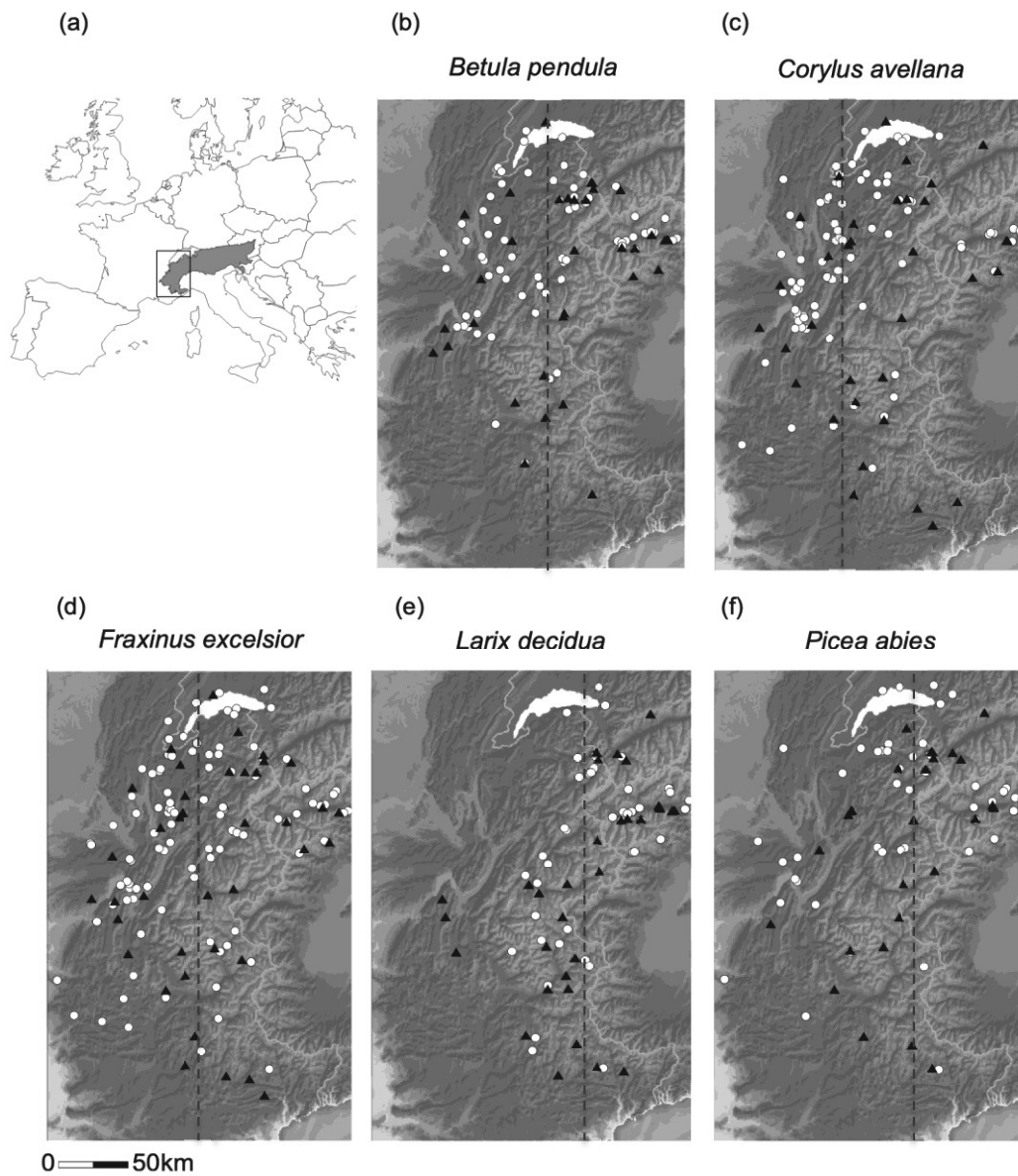
377 We compared the projections of the best models calibrated on observation sites with
378 meteorological stations, in historical (1950-2005) and future climatic conditions (2006 to
379 2100). We used the climatic data generated by the ALADIN-Climat v5 RCM model (CNRM)
380 for the CMIP5 experiment at 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
383 sensitivity analysis of the different model types to climate change and not to provide impact
384 projections. However, we chose the RCP 8.5 scenario because it is close to the current
385 trajectory. Daily minimum and maximum temperatures were extracted for the grid covering
386 the French Alps (43°48'N to 46°47'N, 5°59'E to 7°09'E). We compared the budburst dates
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.

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

393 Budburst dates projected by each model over the 1950-2100 time period were plotted
394 with the associated confidence interval derived from the external validation (see section
395 2.5.1.). The annual / decadal shift of projected budburst dates from Sen's estimator of slope
396 was additionally provided for each model type and each of the 8-km cells in the French Alps
397 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.

400



401

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 *Corylus 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

412

Models compared											
Model type	Correlative					Process-based					
Model family	single variable			bivariate		1-phase			2-phase		Forward calibrated 2-phase
Temperature response	GDD	GDD	TL	GDD +TL	GDD+ TL	GDD	sigmoid	Wang	TL + sigmoid	Wang + sigmoid	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 correlative, 1-phase, 2-phase models + forward calibrated model											
Calibration datasets				meteo sites			east sites		west sites		
Time period				2007-2014							
Model validation: best correlative, 1-phase, 2-phase models + forward calibrated model											
Validation datasets (across space)				no meteo sites			west sites		east sites		
Time period				2007-2014							
Model projection: best correlative, 1-phase, 2-phase models + forward calibrated model											
Projection dataset (across time)				ALADIN-Climat v5 RCM model (CNRM) with RCP 8.5 at 8km resolution							
Time period				1950-2100							

413

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

420

421 3. Results

422 3.1. Selection of the best models

423 Mixed effects models which best explained budburst dates were generally models
424 including GDD5, and chilling as predicting variables (Appendix B). However, budburst dates
425 of *Corylus* 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.

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

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

444 dates) along elevation, except for *Larix* for which observed budburst dates tended to occur
445 earlier than predicted by the models at low elevation and reversely at high elevation
446 (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
449 (Appendix D). This result was confirmed by bootstrapped values of RMSE that were
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.
452 2, Appendix D). However, comparing the performances for an unusually warm year, i.e. with
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

460 Whatever the validation data subset, process-based models provided more accurate
461 projections of the budburst date than correlative models, except for *Picea abies* for which
462 models' performed similarly (Fig. 2, Appendix E). Performances were similar between 2-
463 phase models and 1-phase models. Process-based models were thus more robust than
464 correlative models. Indeed, while RMSE increased from predictions to projections in
465 correlative models, they remained similar in process-based models (Fig. 2, Appendix E).
466 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-based
468 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*

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

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

490 dates (-0.27 to -0.48 days/year; Fig. 4, Appendix K), trend weakened in 1-phase models
491 projection (-0.03 to -0.20 days/year; Fig. 4, Appendix K); and vanished or even reverted in 2-
492 phase 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
497 dates (-32 to -46 days) all along the 1950-2100 period. 1-phase models and 2-phase models
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).

503 For *Fraxinus*, *Betula* and *Picea*, 2-phase models episodically projected budburst
504 failure due to endodormancy release failure because of a lack of chilling. This situation
505 occurred especially at low elevation and with an increasing frequency along the 21th century
506 (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

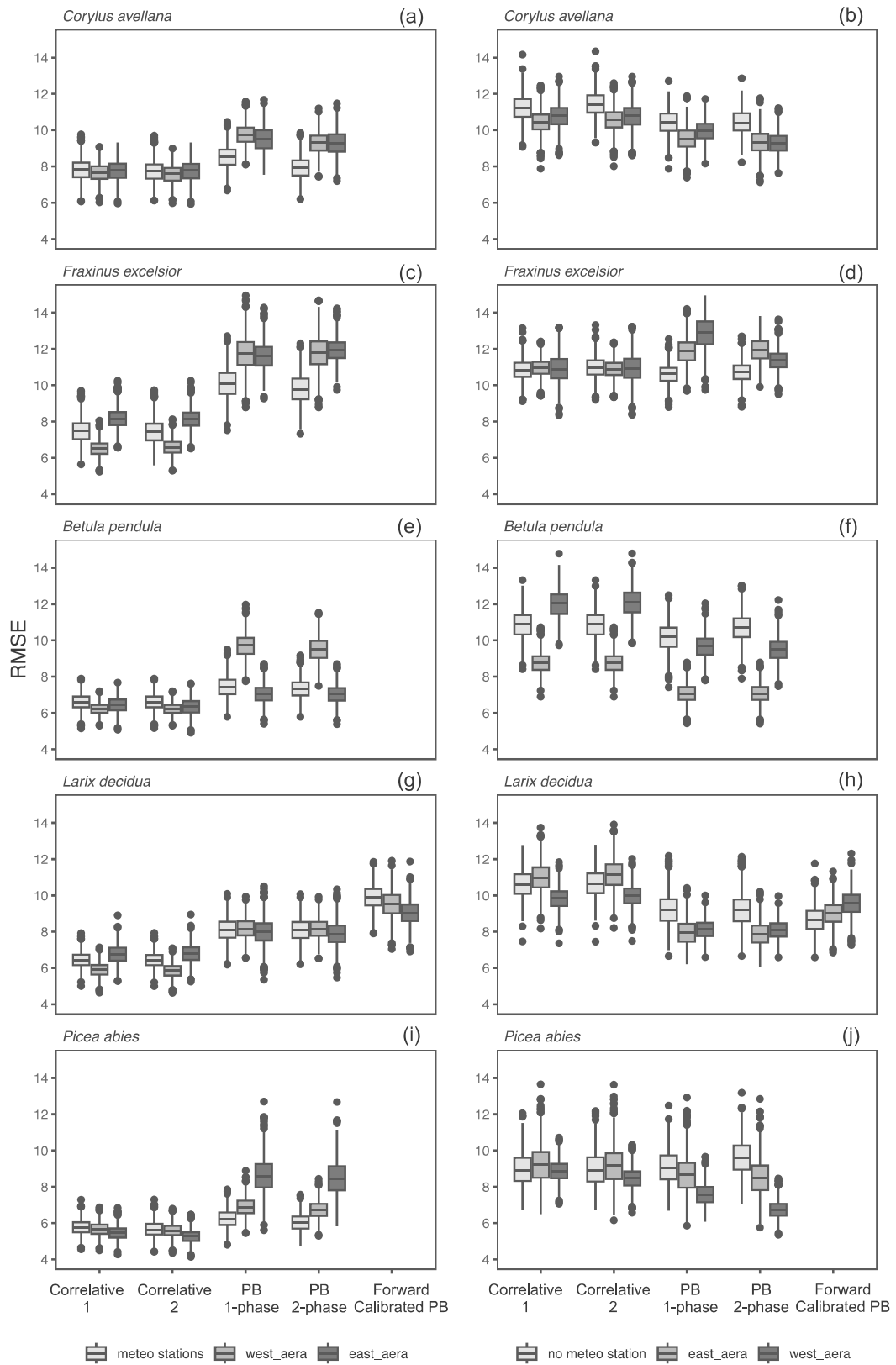
520 The forward calibrated 2-phase model for *Larix* performed the worst on average
521 compared to other models in predicting the budburst date whatever the calibration data subset
522 (Fig. 2, Appendix D), but nevertheless provided more accurate predictions of early dates than
523 the 2-phase model 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
527 data subsets (-0.39 vs +0.65 for 2-phase model and +0.84 for 1-phase model), and thus
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*
530 *decidua*, residuals were linearly related to elevation, with projected dates tending to be
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

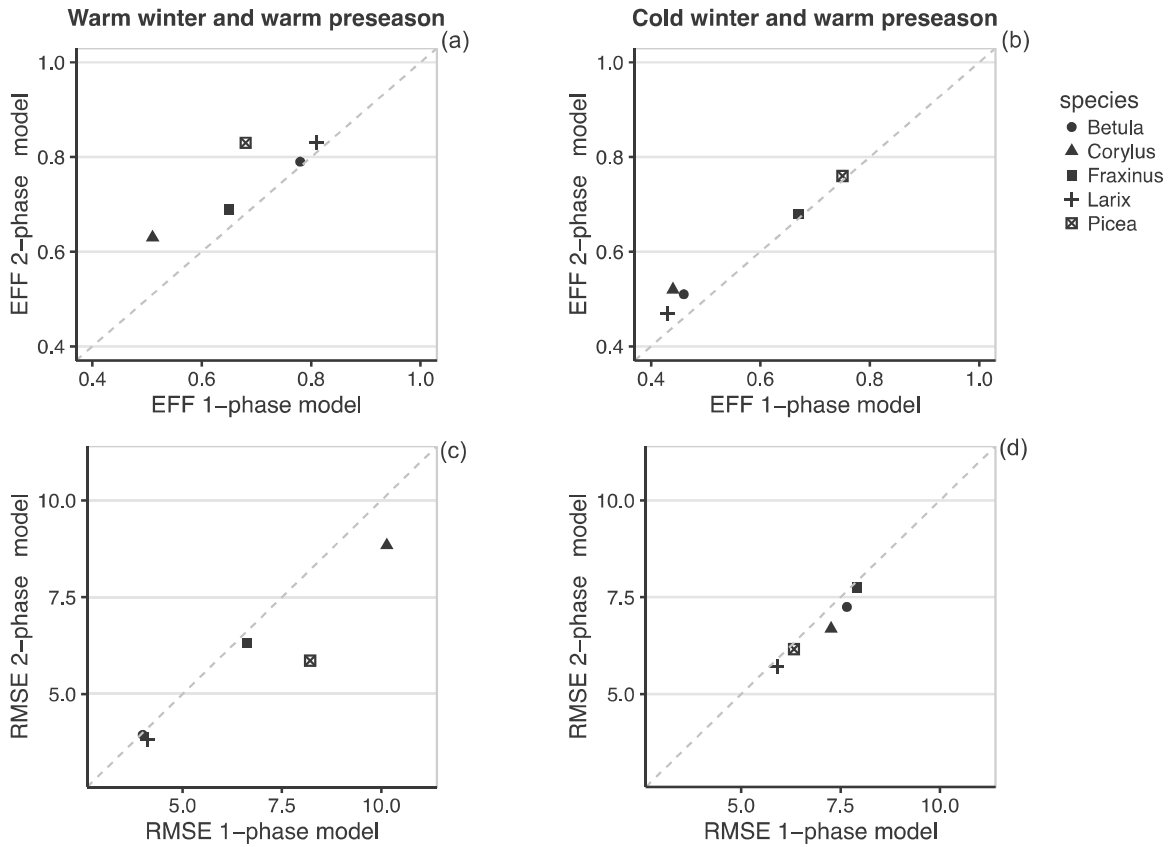
537 projected by the forward calibrated model for *Larix* over the French Alps for each grid cell
538 for the period 1950-2100 (Fig. 6).

Predictions

Projections



540 **Fig. 2:** Boxplots of bootstrapped values of RMSE (days). Performance of the best models in
541 predicting (a, c, e, g, i) and projecting the budburst date (b, d, f, h, j). Predictions correspond
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).
545 Projections correspond to budburst dates predicted by the three different versions of
546 calibrated models for respectively observation sites without meteorological stations (clear
547 grey); observations sites East of the species-specific longitudinal threshold (grey);
548 observation sites West of the species-specific longitudinal threshold (dark grey). Models on
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
552 the linear model with GDD and chilling as variables. PB 1-phase refers to the process-based
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.
555



556

557

558 **Fig. 3:** Performance (Efficiency a, b; RMSE c, d) of the process-based models in predicting

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

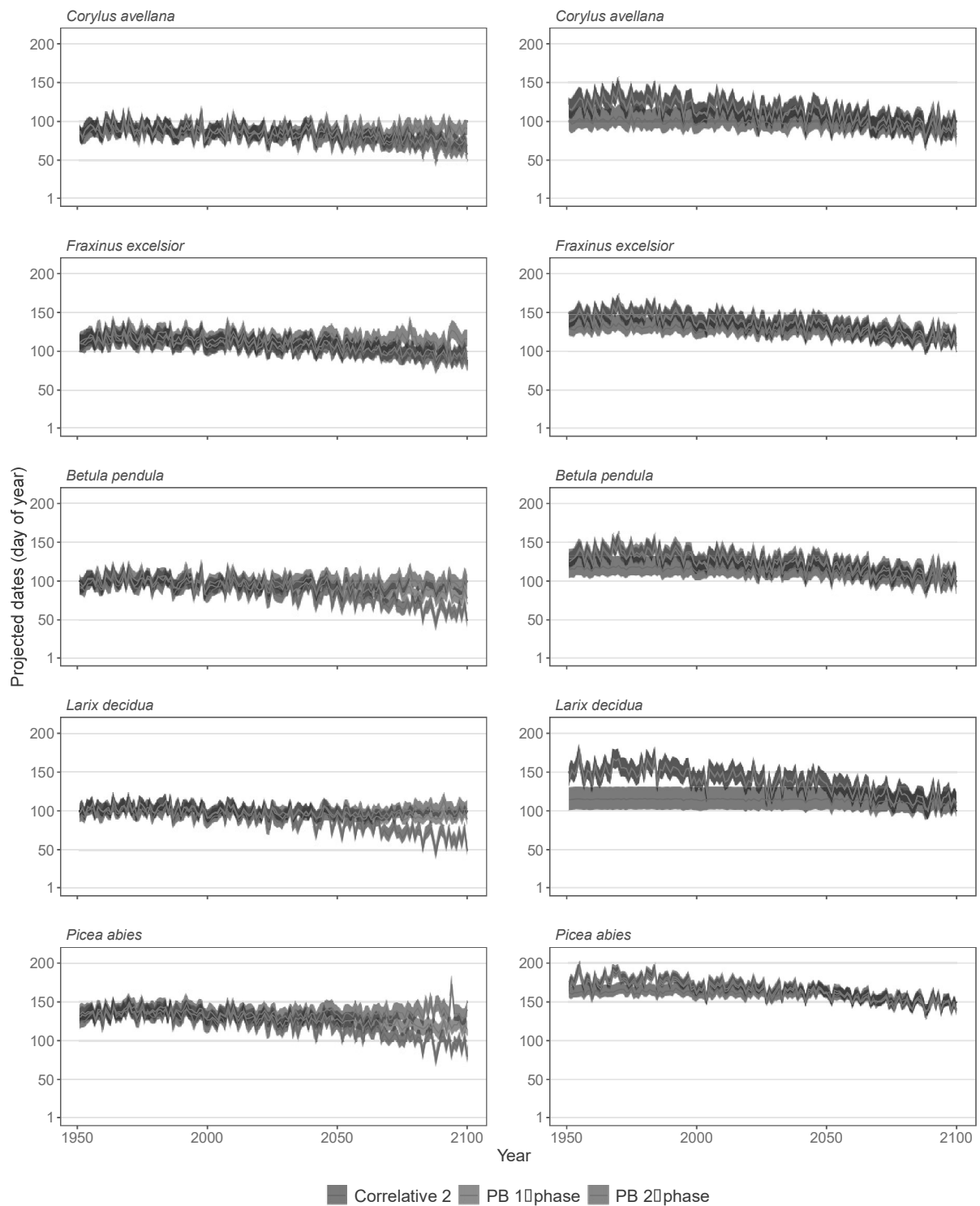
563 threshold function of temperature for the endodormancy phase and a sigmoid function of

564 temperature for the ecodormancy phase. EFF, model efficiency; RMSE, roots-mean-squared

565 error (days). Model labels as in Fig. 2.

566

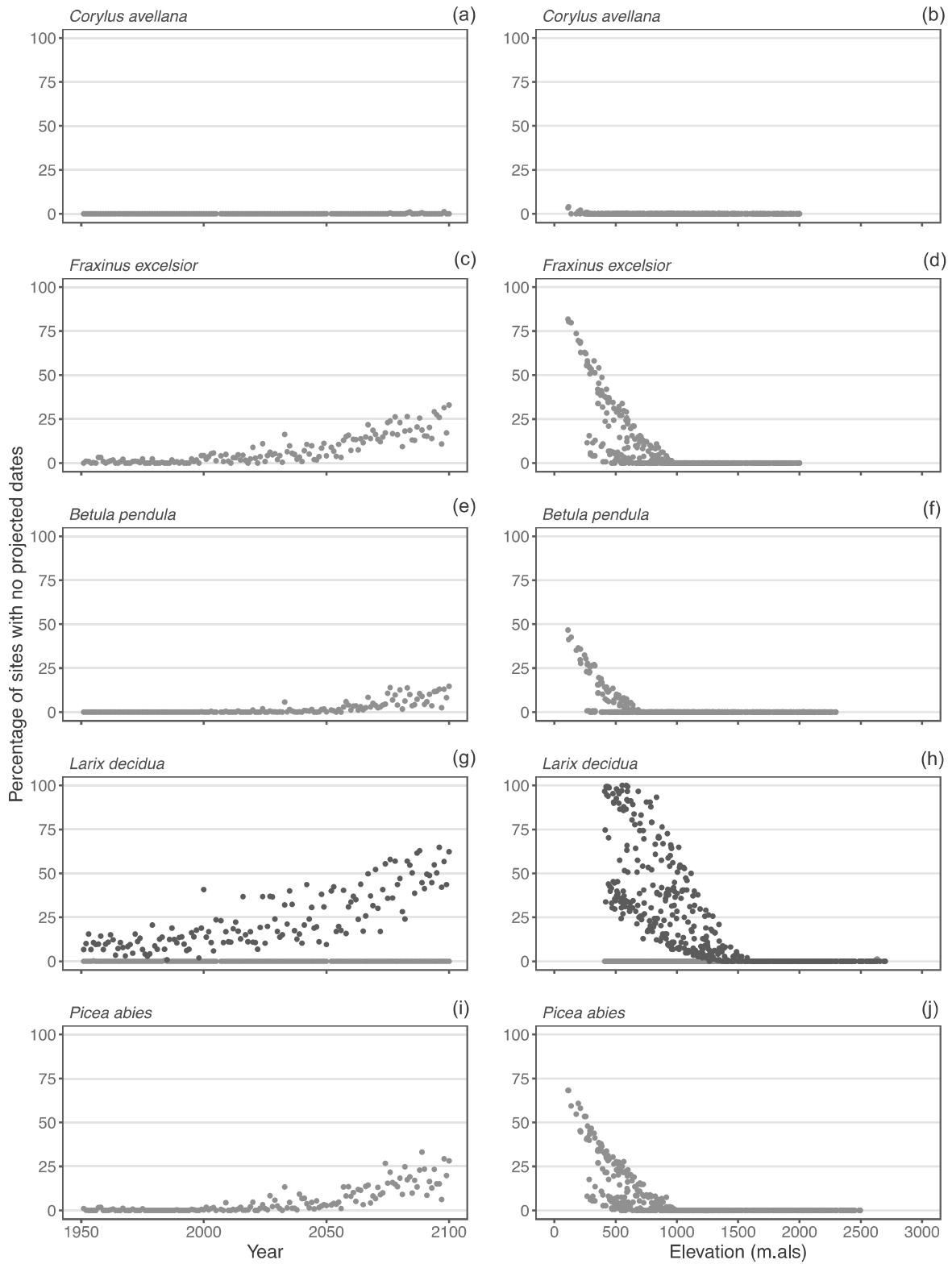
567



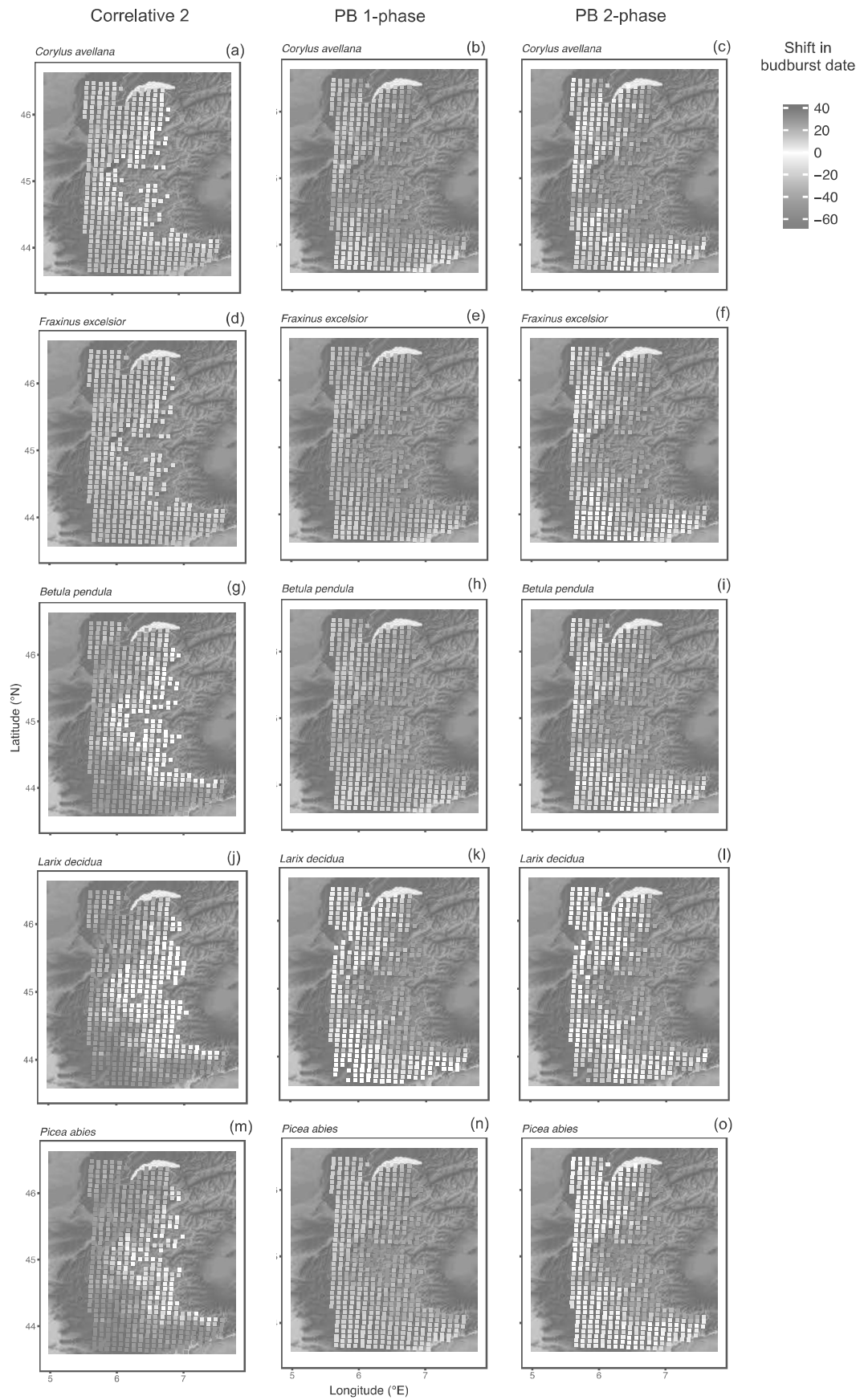
568
569

570 **Fig. 4:** Budburst date projected by the correlative 2 model (with GDD and chilling as variables)
571 (blue), the process-based 1-phase (grey) and the process-based 2-phase model (red) in
572 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.
579

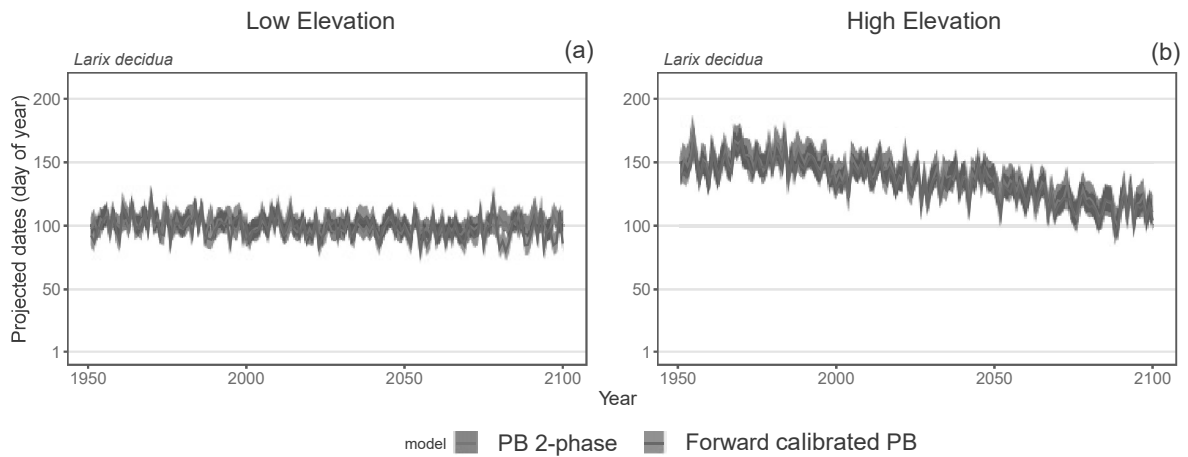


582 **Fig. 5:** Percentage of sites showing dormancy breaking failure under climate scenario
583 RCP8.5 in the Alps along the years (a, c, e, g, i) and along the elevation gradient (b, d, f, h, j).
584 Grey dots indicate values for the process-based 2-phase model and black dots indicate values
585 for 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.
587



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
593 and years over the period 1950 to 2100.
594

595



596
597

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).
601 Red curves indicate the mean date projected by the 2-phase model and red areas indicate the
602 confidence interval of the model. Brown curves indicate the mean date projected by the
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-
607 2100. Model labels as in Fig. 2.

608

609

610 4. Discussion

611 4.1. Process-based phenology models provide more robust projections than correlative 612 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
615 (i.e. *sensu* Randin *et al.*, 2006). However, process-based models were more efficient than
616 correlative models to project budburst date in external conditions (except for *Picea* for which
617 the three model types revealed similar performance). Error in predicted dates and projected
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
626 by their predicting variables.

627 Projections of the forward calibrated 2-phase model were not more accurate than
628 those of the other 2-phase models except for sites without meteorological stations. However,
629 it was the only model that did not show an increased error in external conditions. Increased
630 accuracy in this model was mainly achieved through a more accurate prediction of early
631 dates. Our results show that robustness of process-based models can come additionally from
632 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
637 daily variation of these factors in nature might be poorly represented under controlled
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
641 estimations have both biases that come from the same reason, i.e. incomplete sampling of the
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
648 greenhouses or growth chambers for which temperature and light conditions can be
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

654 Divergence between projections of correlative and 2-phase models in future climatic
655 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,
657 projections were similar. Standard deviations of the projected dates before 2050 for
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
660 elevation gradient. At high elevation, GDD remains low every year, yielding a low variation
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*
671 *al.*, 2008 ; Vitasse *et al.*, 2011). However, 2-phase models provided more accurate
672 predictions of the budburst date for particular recent years with warm winter. This was
673 especially marked for *Corylus* 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
677 negative effect of winter warming on endodormancy release in tree species has been shown in
678 a previous study (Asse *et al.* 2018) and has also been proposed as an explanation of the
679 dampening of the response of budburst to warming temperature over the past 25 years in

680 Europe (Fu et al., 2015). Although warm winter conditions are still rare in our past
681 temperature records, they will become more frequent in the upcoming decades especially
682 after 2050 according to climate projections. Such conditions are expected to delay dormancy
683 release and ultimately delay or even prevent budburst (Fig. 2 & 4). In this context, it becomes
684 essential and urgent that robust 2-phase models be available for as many tree species as
685 possible.

686 Although chilling was taken into account in the correlative models, they did not
687 project a negative effect of a lack of chilling on the budburst date like the 2-phase process-
688 based model. Although the two types of models were calibrated with the same dataset which
689 contained only one exceptionally warm winter (2006-2007) which had a delaying effect on
690 the budburst date (Asse et al., 2018), it seems that only the process-based model was able to
691 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
695 and for all species, with a weak linear trend towards earlier dates (Fig 5 & 6). This linear
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
698 previously highlighted by Vitasse *et al.*, (2011) ; Chuine *et al.*, (2016) and Fig. 1 in Guo et
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.

702 At high elevation, projected budburst dates were similar for all species over the 21st
703 century between 1-phase and 2-phase models, suggesting that at high elevation, chilling
704 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.

715 Our results also support the hypothesis of Vitasse *et al.*, (2017) that winter
716 temperatures are currently actually colder than the optimal chilling temperature at high
717 elevation so that a warming of winter actually increases the number of chilling days and
718 advance endodormancy release, and consequently budburst. Bud endodormancy indeed
719 requires from a few weeks to several months of cold temperature, that can vary from 0°C to
720 12°C depending on the species, to be fully released (Lang *et al.*, 1987; Caffarra *et al.*, 2011a;
721 Malagi *et al.*, 2015).

722 From 1950 to 2100, 2-phase models projected a trend for earlier budburst date in the
723 inner Alps (higher elevations), while they projected either very weak trend toward earlier
724 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.*,
731 2006; Caffarra *et al.*, 2011b; Laube *et al.*, 2014). Additionally to temperature, photoperiod
732 might also co-control budburst in about 30% of temperate tree species (Caffarra *et al.*, 2011;
733 Basler and Körner, 2012; Laube *et al.*, 2014; Zohner and Renner, 2015), with long
734 photoperiod compensating for a lack of chilling. Integration of this compensatory effect in the
735 models might change substantially the projections of budburst dates for the end of the 21st
736 century for photosensitive species which might be the case for *Picea abies* (Blümel &
737 Chmielewski, 2012; Gauzere *et al.*, 2017).

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
746 estimation of model parameters, and we advise using, whenever possible, both backward and
747 forward estimation of model parameters. (3) In opposite to correlative models, process-based

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

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766 **References**

- 767 Anderson, J.J., Gurarie, E., Bracis, C., Burke, B.J., Laidre, K.L., 2013. Modeling climate
768 change impacts on phenology and population dynamics of migratory marine species.
769 *Ecol. Modell.* 264, 83–97. doi:10.1016/j.ecolmodel.2013.03.009
- 770 Asse, D., Chuine, I., Vitasse, Y., Yoccoz, N.G., Delpierre, N., Badeau, V., Delestrade, A.,
771 Randin, C.F., 2018. Warmer winters reduce the advance of tree spring phenology
772 induced by warmer springs in the Alps. *Agric. For. Meteorol.* 252, 220–230.
773 doi:10.1016/j.agrformet.2018.01.030
- 774 Basler, D., 2016. Evaluating phenological models for the prediction of leaf-out dates in six
775 temperate tree species across central Europe. *Agric. For. Meteorol.* 217, 10–21.
776 doi:10.1016/j.agrformet.2015.11.007
- 777 Basler, D., Körner, C., 2012. Photoperiod sensitivity of bud burst in 14 temperate forest tree
778 species. *Agric. For. Meteorol.* 165, 73–81. doi:10.1016/j.agrformet.2012.06.001
- 779 Bellon-Maurel, V., Fernandez-Ahumada, E., Palagos, B., Roger, J.M., McBratney, A., 2010.
780 Critical review of chemometric indicators commonly used for assessing the quality of
781 the prediction of soil attributes by NIR spectroscopy. *TrAC - Trends Anal. Chem.*
782 doi:10.1016/j.trac.2010.05.006
- 783 Benmoussa, H., Ben Mimoun, M., Ghrab, M., Luedeling, E., 2018. Climate change threatens
784 central Tunisian nut orchards. *Int. J. Biometeorol.* 62, 2245–2255. doi:10.1007/s00484-
785 018-1628-x
- 786 Blümel, K., Chmielewski, F.M., 2012. Shortcomings of classical phenological forcing models
787 and a way to overcome them. *Agric. For. Meteorol.* 164, 10–19.
788 doi:10.1016/j.agrformet.2012.05.001
- 789 Bonhomme, M., Rageau, R., Lacoïnte, A., Gendraud, M., 2005. Influences of cold
790 deprivation during dormancy on carbohydrate contents of vegetative and floral
791 primordia and nearby structures of peach buds (*Prunus persica* L. Batch). *Sci. Hortic.*
792 (Amsterdam). 105, 223–240. doi:10.1016/j.scienta.2005.01.015
- 793 Bray, D., Storch, H. Von, 2009. “Prediction” or “Projection”? 534–543.
- 794 Burghardt, L.T., Metcalf, C.J.E., Wilczek, A.M., Schmitt, J., Donohue, K., 2015. Modeling
795 the Influence of Genetic and Environmental Variation on the Expression of Plant Life
796 Cycles across Landscapes. *Am. Nat.* 185, 212–227. doi:10.1086/679439
- 797 Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference: a practical
798 information-theoretic approach, *Ecological Modelling*.
799 doi:10.1016/j.ecolmodel.2003.11.004
- 800 Caffarra, A., Donnelly, A., Chuine, I., 2011a. Modelling the timing of *Betula pubescens*
801 budburst. II. Integrating complex effects of photoperiod into process-based models.
802 *Clim. Res.* 46, 159–170. doi:10.3354/cr00983
- 803 Caffarra, A., Donnelly, A., Chuine, I., Jones, M.B., 2011b. Modelling the timing of *Betula*
804 *pubescens* budburst. I. Temperature and photoperiod: A conceptual model. *Clim. Res.*
805 46, 147–157. doi:10.3354/cr00980
- 806 Cheaib, A., Badeau, V., Boe, J., Chuine, I., Delire, C., Dufrêne, E., François, C., Gritti, E.S.,
807 Legay, M., Pagé, C., Thuiller, W., Viovy, N., Leadley, P., 2012. Climate change impacts
808 on tree ranges: Model intercomparison facilitates understanding and quantification of
809 uncertainty. *Ecol. Lett.* 15, 533–544. doi:10.1111/j.1461-0248.2012.01764.x
- 810 Chuine, I., 2010. Why does phenology drive species distribution? *Philos. Trans. R. Soc. B*
811 *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

814 Chuine, I., Beaubien, E.G., 2001. Phenology is a major determinant of tree species range.
815 *Ecol. Lett.* 4, 500–510. doi:10.1046/j.1461-0248.2001.00261.x

816 Chuine, I., Bonhomme, M., Legave, J.M., Garcia de Cortazar-Atauri, I., Charrier, G.,
817 Lacoite, A., Améglio, T., 2016. Can phenological models predict tree phenology
818 accurately in the future? The unrevealed hurdle of endodormancy break. *Glob. Chang.*
819 *Biol.* 22, 3444–3460. doi:10.1111/gcb.13383

820 Chuine, I., Cour, P., Rousseau, D.D., 1999. Selecting models to predict the timing of
821 flowering of temperate trees: Implications for tree phenology modelling. *Plant, Cell*
822 *Environ.* 22, 1–13. doi:10.1046/j.1365-3040.1999.00395.x

823 Chuine, I., Cour, P., Rousseau, D.D., 1998. Fitting models predicting dates of flowering of
824 temperate-zone trees using simulated annealing. *Plant, Cell Environ.* 21, 455–466.
825 doi:10.1046/j.1365-3040.1998.00299.x

826 Chuine, I., De Cortazar-Atauri, I.G., Kramer, K., Hänninen, H., 2013. Plant development
827 models, in: *Phenology: An Integrative Environmental Science*. pp. 275–293.
828 doi:10.1007/978-94-007-6925-0_15

829 Chuine, I., Régnière, J., 2017. Process-Based Models of Phenology for Plants and Animals.
830 *Annu. Rev. Ecol. Evol. Syst.* 48, 159–182. doi:10.1146/annurev-ecolsys-110316-022706

831 Cianfrani, C., Satizábal, H.F., Randin, C., 2015. A spatial modelling framework for assessing
832 climate change impacts on freshwater ecosystems : Response of brown trout (*Salmo*
833 *trutta L.*) biomass to warming water temperature. *Ecol. Modell.* 313, 1–12.
834 doi:10.1016/j.ecolmodel.2015.06.023

835 Cooke, J.E.K., Weih, M., 2005. Nitrogen storage and seasonal nitrogen cycling in *Populus*:
836 Bridging molecular physiology and ecophysiology. *New Phytol.* doi:10.1111/j.1469-
837 8137.2005.01451.x

838 Dantec, C.F., Vitasse, Y., Bonhomme, M., Louvet, J.M., Kremer, A., Delzon, S., 2014.
839 Chilling and heat requirements for leaf unfolding in European beech and sessile oak
840 populations at the southern limit of their distribution range. *Int. J. Biometeorol.* 58,
841 1853–1864. doi:10.1007/s00484-014-0787-7

842 Delpierre, N., Soudani, K., François, C., Köstner, B., Pontailier, J.Y., Nikinmaa, E., Misson,
843 L., Aubinet, M., Bernhofer, C., Granier, A., Grünwald, T., Heinesch, B., Longdoz, B.,
844 Ourcival, J.M., Rambal, S., Vesala, T., Dufrêne, E., 2009. Exceptional carbon uptake in
845 European forests during the warm spring of 2007: A data-model analysis. *Glob. Chang.*
846 *Biol.* 15, 1455–1474. doi:10.1111/j.1365-2486.2008.01835.x

847 Duputié, A., Rutschmann, A., Ronce, O., Chuine, I., 2015. Phenological plasticity will not
848 help all species adapt to climate change. *Glob. Chang. Biol.* 21, 3062–3073.
849 doi:10.1111/gcb.12914

850 Erez, A., 2000. Bud Dormancy; Phenomenon, Problems and Solutions in the Tropics and
851 Subtropics. *Temp. Fruit Crop. Warm Clim.* 17–48. doi:10.1007/978-94-017-3215-4_2

852 Fu, Y.H., Piao, S., Op de Beeck, M., Cong, N., Zhao, H., Zhang, Y., Menzel, A., Janssens,
853 I.A., 2014. Recent spring phenology shifts in western Central Europe based on
854 multiscale observations. *Glob. Ecol. Biogeogr.* 23, 1255–1263. doi:10.1111/geb.12210

855 Fu, Y.H., Zhao, H., Piao, S., Peaucelle, M., Peng, S., Zhou, G., Ciais, P., Song, Y., Vitasse,
856 Y., Zeng, Z., Janssens, I. a, Huang, M., Menzel, A., Pen, J., 2015. Declining global
857 warming effects on the phenology of spring leaf unfolding. *Nature* 526, 104–107.
858 doi:10.1038/nature15402

859 Gauzere, J., Delzon, S., Davi, H., Bonhomme, M., Garcia de Cortazar-Atauri, I., Chuine, I.,
860 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

864 Guo, L., Dai, J., Wang, M., Xu, J., Luedeling, E., 2015. Responses of spring phenology in
865 temperate zone trees to climate warming: A case study of apricot flowering in China.
866 *Agric. For. Meteorol.* 201, 1–7. doi:10.1016/j.agrformet.2014.10.016

867 Hanninen, H., 1987. Effects of temperature on dormancy release in woody plants:
868 implications of prevailing models. *Silva Fenn.*

869 Higgins, S.I., O’Hara, R.B., Römermann, C., 2012. A niche for biology in species
870 distribution models. *J. Biogeogr.* 39, 2091–2095. doi:10.1111/jbi.12029

871 Hogg, E.H., Price, D.T., Black, T.A., 2000. Postulated feedbacks of deciduous forest
872 phenology on seasonal climate patterns in the Western Canadian interior. *J. Clim.* 13,
873 4229–4243. doi:10.1175/1520-0442(2000)013<4229:PFODFP>2.0.CO;2

874 Howe, G.T., Saruul, P., Davis, J., Chen, T.H.H., 2000. Quantitative genetics of bud
875 phenology, frost damage, and winter survival in an F 2 family of hybrid poplars. *TAG*
876 *Theor. Appl. Genet.* 101, 632–642. doi:10.1007/s001220051525

877 Janssen, P.H.M., Heuberger, P.S.C., 1995. Calibration of process-oriented models. *Ecol.*
878 *Modell.* 83, 55–66. doi:10.1016/0304-3800(95)00084-9

879 Jones, H.G., Hillis, R.M., Gordon, S.L., Brennan, R.M., 2013. An approach to the
880 determination of winter chill requirements for different *Ribes* cultivars. *Plant Biol.* 15,
881 18–27. doi:10.1111/j.1438-8677.2012.00590.x

882 Kearney, M.R., Wintle, B.A., Porter, W.P., 2010. Correlative and mechanistic models of
883 species distribution provide congruent forecasts under climate change. *Conserv. Lett.* 3,
884 203–213. doi:10.1111/j.1755-263X.2010.00097.x

885 Kollas, C., Randin, C.F., Vitasse, Y., Körner, C., 2014. Agricultural and Forest Meteorology
886 How accurately can minimum temperatures at the cold limits of tree species be
887 extrapolated from weather station data ? *Agric. For. Meteorol.* 184, 257–266.
888 doi:10.1016/j.agrformet.2013.10.001

889 Körner, C., 1999. Alpine plant life: functional plant ecology of high mountain ecosystems,
890 Alpine plant life functional plant ecology of high mountain ecosystems.
891 doi:10.1659/0276-4741(2001)021[0202:APLFPE]2.0.CO;2

892 Lang, G., Early, J., Martin, G., Darnell, R., 1987. Endo-, para-, and ecodormancy:
893 physiological terminology and classification for dormancy research. *HortScience.*

894 Laube, J., Sparks, T.H., Estrella, N., Höfler, J., Ankerst, D.P., Menzel, A., 2014. Chilling
895 outweighs photoperiod in preventing precocious spring development. *Glob. Chang. Biol.*
896 20, 170–182. doi:10.1111/gcb.12360

897 Lebourgeois, F., Pierrat, J.C., Perez, V., Piedallu, C., Cecchini, S., Ulrich, E., 2010.
898 Simulating phenological shifts in French temperate forests under two climatic change
899 scenarios and four driving global circulation models. *Int. J. Biometeorol.* 54, 563–581.
900 doi:10.1007/s00484-010-0305-5

901 Lindstrom, M., Bates, D., 1990. Nonlinear mixed effects models for repeated measures data.
902 *Biometrics.* doi:10.2307/2532087

903 Linkosalo, T., Lappalainen, H.K., Hari, P., 2008. A comparison of phenological models of
904 leaf bud burst and flowering of boreal trees using independent observations. *Tree*
905 *Physiol.* 28, 1873–1882. doi:10.1093/treephys/28.12.1873

906 Lobell, D.B., Burke, M.B., 2010. On the use of statistical models to predict crop yield
907 responses to climate change. *Agric. For. Meteorol.* 150, 1443–1452.
908 doi:10.1016/j.agrformet.2010.07.008

- 909 Luedeling, E., Zhang, M., McGranahan, G., Leslie, C., 2009. Validation of winter chill
910 models using historic records of walnut phenology. *Agric. For. Meteorol.* 149, 1854–
911 1864. doi:10.1016/j.agrformet.2009.06.013
- 912 Malagi, G., Sachet, M.R., Citadin, I., Herter, F.G., Bonhomme, M., Regnard, J.L., Legave,
913 J.M., 2015. The comparison of dormancy dynamics in apple trees grown under
914 temperate and mild winter climates imposes a renewal of classical approaches. *Trees -*
915 *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.,
917 Bissolli, P., Braslavská, O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y.,
918 Dahl, Å., Defila, C., Donnelly, A., Filella, Y., Jatczak, K., Måge, F., Mestre, A., Nordli,
919 Ø., Peñuelas, J., Pirinen, P., Remišová, V., Scheifinger, H., Striz, M., Susnik, A., Van
920 Vliet, A.J.H., Wielgolaski, F.E., Zach, S., Zust, A., 2006. European phenological
921 response to climate change matches the warming pattern. *Glob. Chang. Biol.* 12, 1969–
922 1976. doi:10.1111/j.1365-2486.2006.01193.x
- 923 Morin, X., Thuiller, W., 2009. Comparing niche- and process-based models to reduce
924 prediction uncertainty in species range shifts under climate change. *Ecology* 90, 1301–
925 1313. doi:10.1890/08-0134.1
- 926 Mountain Research Initiative EDW Working Group, 2015. Elevation-dependent warming in
927 mountain regions of the world. *Nat. Clim. Chang.* 5, 424–430.
928 doi:10.1038/nclimate2563\rhttp://www.nature.com/nclimate/journal/v5/n5/abs/nclimate
929 2563.html#supplementary-information
- 930 Nagano, A.J., Sato, Y., Mihara, M., Antonio, B.A., Motoyama, R., Itoh, H., Nagamura, Y.,
931 Izawa, T., 2012. Deciphering and prediction of transcriptome dynamics under
932 fluctuating field conditions. *Cell* 151, 1358–1369. doi:10.1016/j.cell.2012.10.048
- 933 Nash, J.E., Sutcliffe, J. V., 1970. River flow forecasting through conceptual models part I - A
934 discussion of principles. *J. Hydrol.* 10, 282–290. doi:10.1016/0022-1694(70)90255-6
- 935 Nissanka, S.P., Karunaratne, A.S., Perera, R., Weerakoon, W.M.W., Thorburn, P.J., Wallach,
936 D., 2015. Calibration of the phenology sub-model of APSIM-Oryza: Going beyond
937 goodness of fit. *Environ. Model. Softw.* 70, 128–137. doi:10.1016/j.envsoft.2015.04.007
- 938 Olesen, J.E., Trnka, M., Kersebaum, K.C., Skjelvåg, A.O., Seguin, B., Peltonen-Sainio, P.,
939 Rossi, F., Kozyra, J., Micale, F., 2011. Impacts and adaptation of European crop
940 production systems to climate change. *Eur. J. Agron.* 34, 96–112.
941 doi:10.1016/j.eja.2010.11.003
- 942 Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts
943 across natural systems. *Nature* 421, 37–42. doi:10.1038/nature01286
- 944 Petri, J.L., Leite, G.B., 2004. Consequences of insufficient winter chilling on apple tree bud-
945 break, in: *Acta Horticulturae*. pp. 53–60. doi:10.17660/ActaHortic.2004.662.4
- 946 Pinheiro, J.C., Bates, D.M., 1996. Unconstrained parametrizations for variance-covariance
947 matrices. *Stat. Comput.* 6, 289–296. doi:10.1007/BF00140873
- 948 R Core Team, 2016. R: A language and environment for statistical computing. Version 3.3.2.
949 R Found. Stat. Comput. Vienna, Austria. doi:10.1017/CBO9781107415324.004
- 950 Randin, C.F., Dirnböck, T., Dullinger, S., Zimmermann, N.E., Zappa, M., Guisan, A., 2006.
951 Are niche-based species distribution models transferable in space? *J. Biogeogr.* 33,
952 1689–1703. doi:10.1111/j.1365-2699.2006.01466.x
- 953 Rebetez, M., Reinhard, M., 2008. Monthly air temperature trends in Switzerland 1901-2000
954 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,
959 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.1365-2486.2011.02562.x

963 Satake, A., Kawagoe, T., Saburi, Y., Chiba, Y., Sakurai, G., Kudoh, H., 2013. Forecasting
964 flowering phenology under climate warming by modelling the regulatory dynamics of
965 flowering-time genes. *Nat. Commun.* 4. doi:10.1038/ncomms3303

966 Schaber, J., Badeck, F.W., 2003. Physiology-based phenology models for forest tree species
967 in Germany. *Int. J. Biometeorol.* 47, 193–201. doi:10.1007/s00484-003-0171-5

968 Sen, P.K., 1968. Estimates of the Regression Coefficient Based on Kendall's Tau. *J. Am.*
969 *Stat. Assoc.* 63, 1379–1389. doi:10.1080/01621459.1968.10480934

970 Vitasse, Y., 2013. Ontogenic changes rather than difference in temperature cause understory
971 trees to leaf out earlier. *New Phytol.* 198, 149–155. doi:10.1111/nph.12130

972 Vitasse, Y., François, C., Delpierre, N., Dufrêne, E., Kremer, A., Chuine, I., Delzon, S., 2011.
973 Assessing the effects of climate change on the phenology of European temperate trees.
974 *Agric. For. Meteorol.* 151, 969–980. doi:10.1016/j.agrformet.2011.03.003

975 Vitasse, Y., Rebetez, M., Filippa, G., Cremonese, E., Klein, G., Rixen, C., 2016. 'Hearing'
976 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

980 Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin,
981 J.M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate
982 change. *Nature* 416, 389–395. doi:10.1038/416389a

983 Wang, E., Engel, T., 1998. Simulation of phenological development of wheat crops. *Agric.*
984 *Syst.* 58, 1–24. doi:10.1016/S0308-521X(98)00028-6

985 Zguigal, A., Chahbar, A., Loudiyi, D.E.M.W., Crabbé, J., 2006. Caractéristiques de la
986 dormance des bourgeons du pommier dans les régions à hiver doux. *Biotechnol. Agron.*
987 *Soc. Environ.* 10, 131–137.

988 Zohner, C.M., Benito, B.M., Svenning, J.C., Renner, S.S., 2016. Day length unlikely to
989 constrain climate-driven shifts in leaf-out times of northern woody plants. *Nat. Clim.*
990 *Chang.* 6, 1120–1123. doi:10.1038/nclimate3138

991 Zohner, C.M., Renner, S.S., 2015. Perception of photoperiod in individual buds of mature
992 trees regulates leaf-out. *New Phytol.* 208, 1023–1030. doi:10.1111/nph.13510

993 Zohner, C.M., Renner, S.S., 2014. Common garden comparison of the leaf-out phenology of
994 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**

1000 Phenoclim is a citizen science program initiated in 2004 (www.phenoclim.org) by CREA
1001 (Centre de Recherches sur les Ecosystèmes d'Altitude, Chamonix, France), which aims at
1002 assessing the long-term effects of climate change on plant phenology over the French Alps.
1003 The specificity of this program, compared to other existing citizen science initiatives, lies not
1004 only in its large geographic coverage in mountain environments, but also in its simultaneous
1005 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
1011 observations were recorded weekly. For each species, yearly budburst dates were calculated
1012 as the mean date of individuals observed at a given site. The five surveyed species do not
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.

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Appendix B

Linear mixed models of budburst dates as response variables and temperature-based factors as competing predicting variables. Models are calibrated both on observation sites equipped with temperature stations and on all observation sites. Adjusted R-squared (R^2), AIC, and P -value of ANOVA are provided for each model. Var-part= partitions of variance between growing degree-days $> 0^\circ\text{C}$ (GDD0), growing degree-days $> 5^\circ\text{C}$ (GGD5), and chilling. For models with both GDD and chilling, two P values are provided, one for each effect.

	Budburst													
	With temperature stations					All sites								
	<i>N</i>	AIC	R^2	<i>P</i> -value (anova)	Var-part GDD0	Var-part chilling	Var-part - both	<i>N</i>	AIC	R^2	<i>P</i> -value (anova)	Var-part GDD0	Var-part chilling	Var-part - both
<i>C. avellana</i>	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	***/NS	0.30	0.01	0.11		2373	0.62	***/NS	0.28	0.0	0.18
GDD5+Chilling		932	0.52	***/NS	0.24	0.01	0.12		2392	0.60	***/**	0.23	0.0	0.18
<i>F. excelsior</i>	152							396						
GDD0		1132	0.65	***					2949	0.70	***			
GDD5		1133	0.65	***					2958	0.70	***			
Chilling		1174	0.50	*					3106	0.53	***			
GDD0+Chilling		1126	0.64	***/NS	0.24	0.0	0.22		2944	0.70	***/NS	0.23	0.0	0.33
GDD5+Chilling		1127	0.65	***/NS	0.23	0.0	0.22		2953	0.70	***/NS	0.22	0.0	0.33
<i>B. pendula</i>	145							307						
GDD0		1052	0.72	***					2224	0.76	***			
GDD5		1049	0.73	***					2227	0.76	***			
Chilling		1120	0.54	*					2393	0.55	***			
GDD0+Chilling		1047	0.72	***/NS	0.34	0.0	0.2		2220	0.76	***/NS	0.32	0.0	0.23
GDD5+Chilling		1044	0.73	***/NS	0.35	0.1	0.3		2222	0.76	***/NS	0.33	0.0	0.23
<i>L. decidua</i>	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	***/NS	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
<i>P. abies</i>	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	***/NS	0.50	0.01	0.15		1752	0.81	***/NS	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 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; SS_{tot} total variance (sum of squares), SS_{res} residual variance (sum of squares); RMSE Root mean squared error; EFF efficiency; AICc Corrected Akaike's Information Criteria.

Species	1-phase model			2-phase model		
	GDD	Sigmoid	Wang	Threshold lower/sigmoid	Wang/sigmoid	
<i>C. avellana</i> Parameters	$t_0 = 1$	$t_0 = 57$	$t_0 = 51$	$t_0 = -115$	$t_0 = -119$	
	$F^* = 21$	$F^* = 8$	$F^* = 6$	$C^* = 145$	$C^* = 150$	
	$T_b = 7.12$	$d_T = -0.45$	$T_{opt} = 27.95$	$F^* = 11$	$F^* = 4$	
		$T_{50} = 8.44$	$T_{min} = -2.94$	$T_h = 16$	$T_{opt} = 5.07$	
			$T_{max} = 41.13$	$d_T = -0.38$	$T_{min} = -4.47$	
				$T_{50} = 8.61$	$T_{max} = 22.07$	
					$d_T = -1.71$	
					$T_{50} = 7.91$	
	<i>Calibration performances</i>					
	N	128	128	128	128	128
	k	3	4	5	6	8
	SS_{tot}	22262	19743	19743	19743	19743
	SS_{res}	16559	9815	9796	8564	7470
RMSE	10.91	8.76	8.75	8.18	7.64	
EFF	0.26	0.5	0.5	0.57	0.62	
AICc	626.51	563.80	565.72	550.72	537.74	
<i>F. excelsior</i> Parameters	$t_0 = 1$	$t_0 = 54.7$	$t_0 = 55$	$t_0 = -77$	$t_0 = -78$	
	$F^* = 121$	$F^* = 17$	$F^* = 23$	$C^* = 125$	$C^* = 125$	
	$T_b = 5.68$	$d_T = -0.22$	$T_{opt} = 16.2$	$F^* = 9$	$F^* = 9$	
		$T_{50} = 12.25$	$T_{min} = -38.8$	$T_h = 10.6$	$T_{opt} = 0.1$	
			$T_{max} = 20.8$	$d_T = -0.2$	$T_{min} = -36.6$	
				$T_{50} = 16.2$	$T_{max} = 21.3$	
					$d_T = -0.24$	
					$T_{50} = 10.41$	
	<i>Calibration performances</i>					
	N	149	149	149	149	149
	k	3	4	5	6	8
	SS_{tot}	34545	31275	31275	31275	31275
	SS_{res}	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	
<i>B. pendula</i> Parameters	$t_0 = 1$	$t_0 = 60$	$t_0 = 62$	$t_0 = -101$	$t_0 = -108$	
	$F^* = 72$	$F^* = 1$	$F^* = 9$	$C^* = 127$	$C^* = 157$	
	$T_b = 4.9$	$d_T = -0.2$	$T_{opt} = 17.4$	$F^* = 5$	$F^* = 5$	
		$T_{50} = 24.5$	$T_{min} = -37.5$	$T_h = 12.2$	$T_{opt} = 3.4$	
			$T_{max} = 21.5$	$d_T = -0.2$	$T_{min} = -9.9$	
				$T_{50} = 16.97$	$T_{max} = 26.2$	
					$d_T = -0.2$	
					$T_{50} = 14.7$	
	<i>Calibration performances</i>					
	N	146	146	146	146	146
	k	3	4	5	6	8
	SS_{tot}	30844	30313	30313	30313	30313
	SS_{res}	14743	8425	8440	8298	7720
RMSE	9.69	7.6	7.6	7.5	7.27	
EFF	0.52	0.72	0.72	0.73	0.75	
AICc	677.86	600.36	601.89	602.46	596.38	

Species		1-phase model			2-phase model	
		GDD	Sigmoid	Wang	Threshold lower/sigmoid	Wang/sigmoid
<i>L. decidua</i>	<i>Parameters</i>	$t_0 = 1$	$t_0 = 83$	$t_0 = 83$	$t_0 = -100.8$	$t_0 = 66$
		$F^* = 3$	$F^* = 6$	$F^* = 6$	$C^* = 184$	$C^* = 134$
		$T_b = 9.6$	$d_T = -37$	$T_{opt} = 10.1$	$F^* = 6$	$F^* = 6$
			$T_{50} = 6.2$	$T_{min} = 5.9$	$T_h = 18.3$	$T_{opt} = 9$
				$T_{max} = 37.7$	$d_T = -37.4$	$T_{min} = -38.9$
					$T_{50} = 6.2$	$T_{max} = 34.2$
						$d_T = -7.1$
					$T_{50} = 6.2$	
		<i>Calibration performances</i>				
		N	159	159	159	159
		k	3	4	5	6
		SS _{tot}	27728	26275	26275	26275
		SS _{res}	54044	11328	11240	11297
	RMSE	17.83	8.44	8.41	8.43	
	EFF	-0.95	0.57	0.57	0.57	
	AIC _c	930.83	686.58	687.47	690.43	
<i>P. abies</i>	<i>Parameters</i>	$t_0 = 1$	$t_0 = 83$	$t_0 = 84$	$t_0 = -100$	$t_0 = -107$
		$F^* = 290$	$F^* = 5$	$F^* = 8$	$C^* = 174$	$C^* = 176$
		$T_b = 2.96$	$d_T = -0.1$	$T_{opt} = 29.9$	$F^* = 8$	$F^* = 3$
			$T_{50} = 24.2$	$T_{min} = -36.3$	$T_h = 13.9$	$T_{opt} = 0.01$
				$T_{max} = 37.6$	$d_T = -0.2$	$T_{min} = -39.8$
					$T_{50} = 18.1$	$T_{max} = 24.9$
						$d_T = -0.2$
					$T_{50} = 27.6$	
		<i>Calibration performances</i>				
		N	112	112	112	112
		k	3	4	5	6
		SS _{tot}	22158	21453	21453	21453
		SS _{res}	10623	4989	4984	4660
	RMSE	9.29	6.67	6.67	6.45	
	EFF	0.52	0.77	0.77	0.78	
	AIC _c	513.97	433.58	435.66	430.36	

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 to observations sites West of the species-specific longitudinal threshold; East sites refers to observation sites East of the species-specific longitudinal threshold. 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, root-mean-squared error (days); RMSEs, systematic root mean square error (days); RPIQ, ratio of performance to interquartile distance; N, number of data used to fit the model.

	Meteo sites						West sites						East sites						
	AICc	EFF	RMSE	RMSEs	RPIQ	N	AICc	EFF	RMSE	RMSEs	RPIQ	N	AICc	EFF	RMSE	RMSEs	RPIQ	N	
<i>Betula</i>																			
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	999.7	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	
<i>Corylus</i>																			
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	
<i>Fraxinus</i>																			
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	
<i>Larix</i>																			
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	6.69	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	
<i>Picea</i>																			
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	

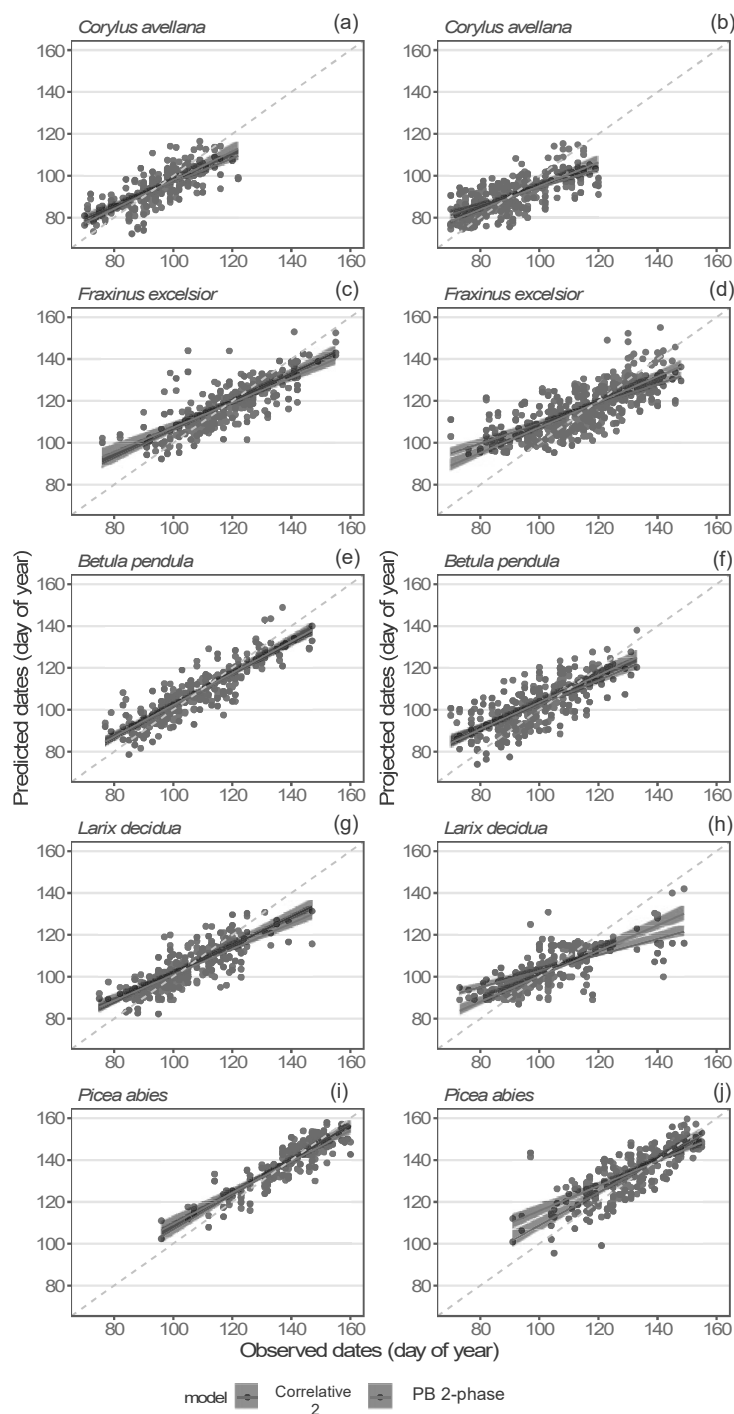
Appendix E

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 stations					West sites					East sites												
	No meteo station					East sites					West sites												
	R^2	RMSE	RMSEs	RPIQ	Diff RMSE	R^2	RMSE	RMSEs	RPIQ	Diff RMSE	R^2	RMSE	RMSEs	RPIQ	Diff RMSE	R^2	RMSE	RMSEs	RPIQ	Diff RMSE	N		
<i>Betula</i>																							
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					
<i>Corylus</i>																							
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					
<i>Fraxinus</i>																							
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					
<i>Larix</i>																							
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					
<i>Picea</i>																							
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					

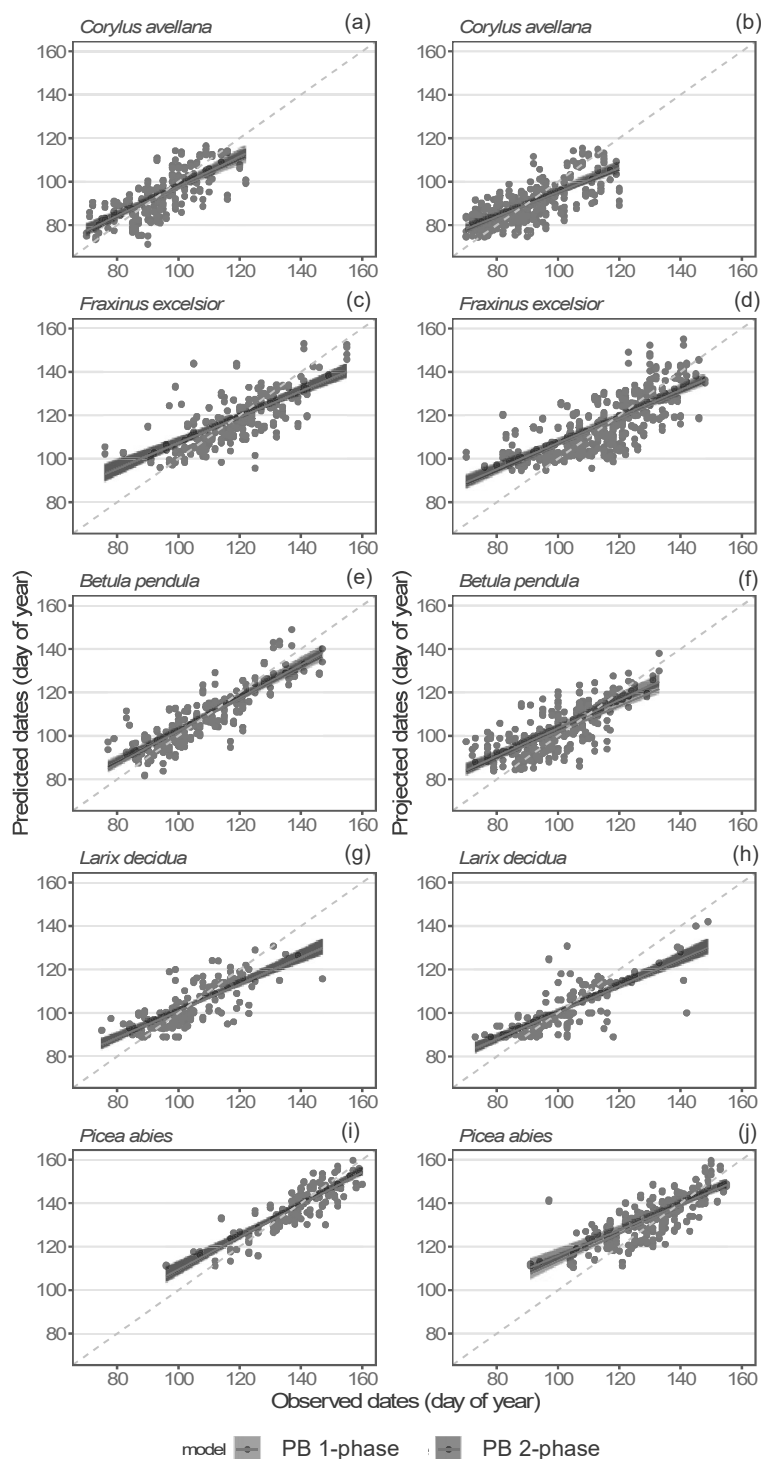
Appendix F

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.



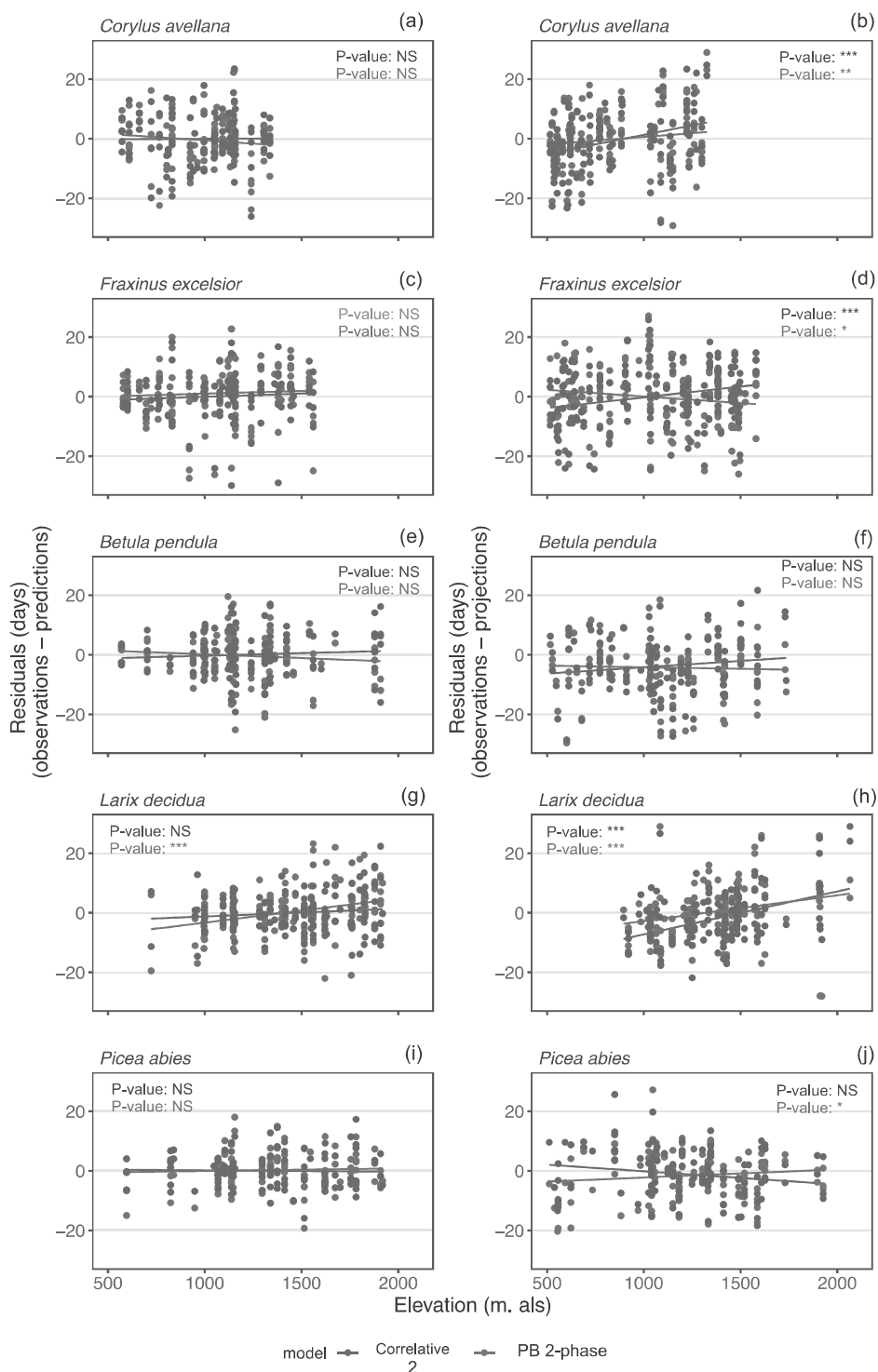
Appendix G

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.



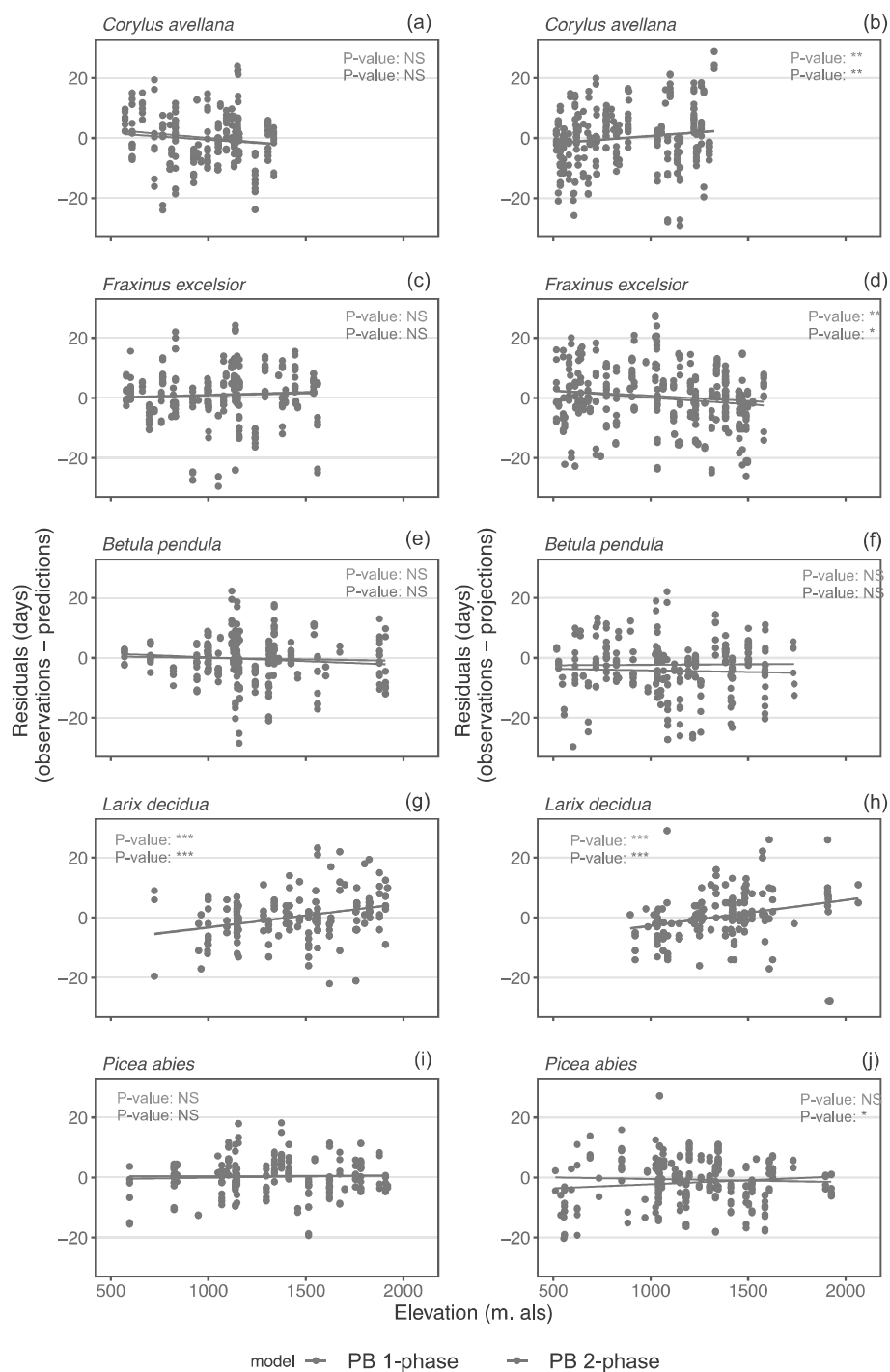
Appendix H

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).



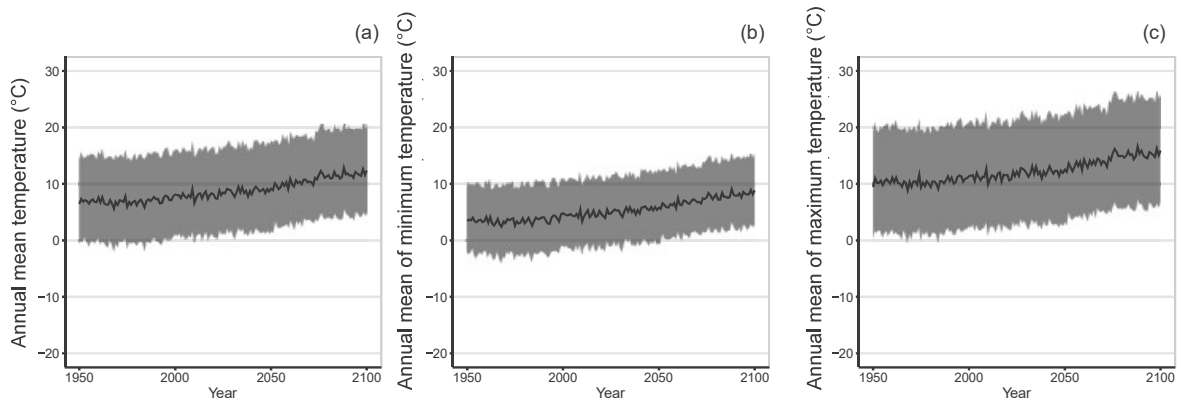
Appendix I

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 (<http://drias-climat.fr/>). 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.



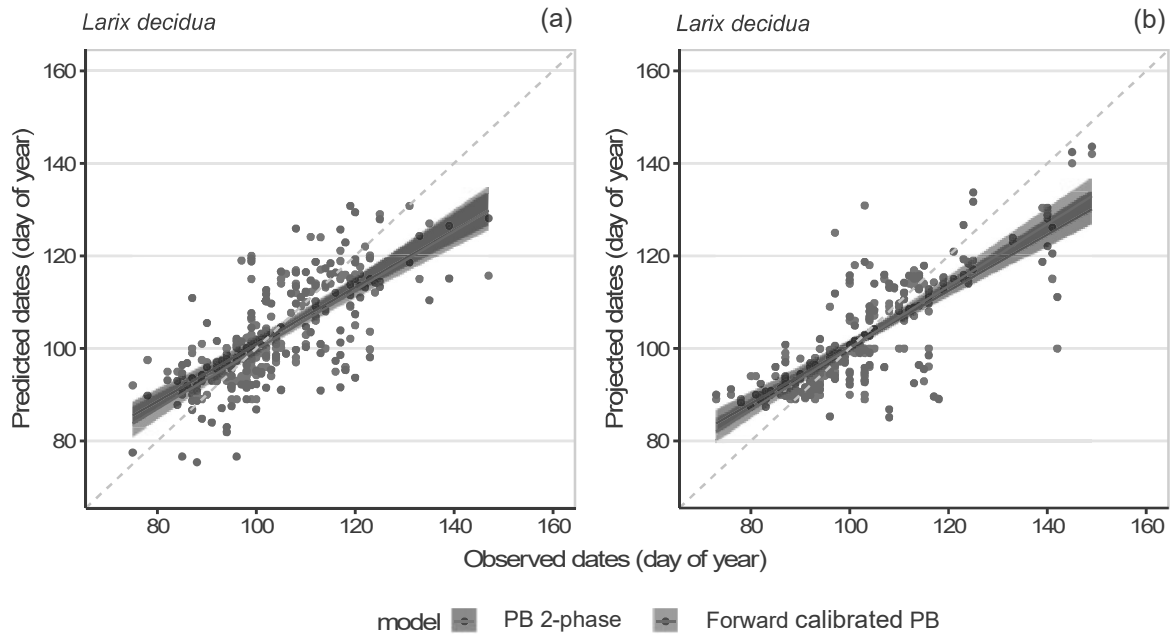
Appendix K

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 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).

Species	Model	Low elevation						High elevation					
		1950-2100		1950-2050		2050-2100		1950-2100		1950-2050		2050-2100	
		trend	trendp	trend	trendp	trend	trendp	trend	trendp	trend	trendp	trend	trendp
<i>C. avellana</i>	<i>Correlative</i>	-0.15	-22.90	-0.08	-7.50	-0.27	-13.90	-0.08	-12.00	-0.03	-3.20	-0.20	-10.40
	<i>Process-based 1-phase</i>	-0.13	-19.30	-0.10	-9.30	-0.17	-8.70	-0.26	-37.80	-0.17	-16.80	-0.37	-18.50
	<i>Process-based 2-phase</i>	-0.02	-2.50	-0.05	-4.60	0.08	3.90	-0.23	-34.40	-0.17	-16.50	-0.29	-14.50
<i>F. excelsior</i>	<i>Correlative</i>	-0.16	-24.30	-0.10	-10.10	-0.27	-13.80	-0.12	-17.70	-0.07	-6.60	-0.25	-12.60
	<i>Process-based 1-phase</i>	-0.16	-23.10	-0.12	-11.30	-0.20	-10.00	-0.23	-34.60	-0.16	-15.80	-0.32	-16.20
	<i>Process-based 2-phase</i>	-0.05	-7.90	-0.07	-6.80	0.020	0.80	-0.21	-31.80	-0.16	-15.30	-0.27	-13.60
<i>B. pendula</i>	<i>Correlative</i>	-0.25	-37.70	-0.15	-14.60	-0.45	-23.10	-0.10	-15.20	-0.05	-4.50	-0.28	-14.50
	<i>Process-based 1-phase</i>	-0.14	-20.10	-0.10	-9.50	-0.19	-9.40	-0.23	-34.00	-0.16	-15.50	-0.33	-16.50
	<i>Process-based 2-phase</i>	-0.04	-5.70	-0.05	-4.60	-0.01	-0.50	-0.22	-32.60	-0.16	-15.60	-0.28	-13.80
<i>L. decidua</i>	<i>Correlative</i>	-0.24	-35.70	-0.13	-13.10	-0.47	-24.20	-0.02	-3.60	-0.01	-0.50	-0.13	-6.90
	<i>Process-based 1-phase</i>	-0.09	-13.00	-0.09	-9.30	-0.03	-1.30	-0.31	-46.20	-0.20	-19.70	-0.42	-20.90
	<i>Process-based 2-phase</i>	-0.02	-3.30	-0.07	-7.10	0.16	8.20	-0.31	-46.60	-0.21	-20.10	-0.41	-20.80
	<i>Forward calibrated PB</i>	-0.05	-8.10	-0.01	-1.10	-0.02	-1.10	-0.29	-43.40	-0.20	-19.60	-0.38	-19.10
<i>P. abies</i>	<i>Correlative</i>	-0.27	-40.60	-0.16	-16.30	-0.48	-24.40	-0.08	-12.70	-0.03	-3.00	-0.25	-12.80
	<i>Process-based 1-phase</i>	-0.14	-21.20	-0.11	-11.10	-0.19	-9.70	-0.25	-37.30	-0.17	-17.00	-0.32	-16.00
	<i>Process-based 2-phase</i>	-0.03	-3.80	-0.05	-5.30	0.10	5.10	-0.26	-38.80	-0.18	-18.00	-0.32	-15.80

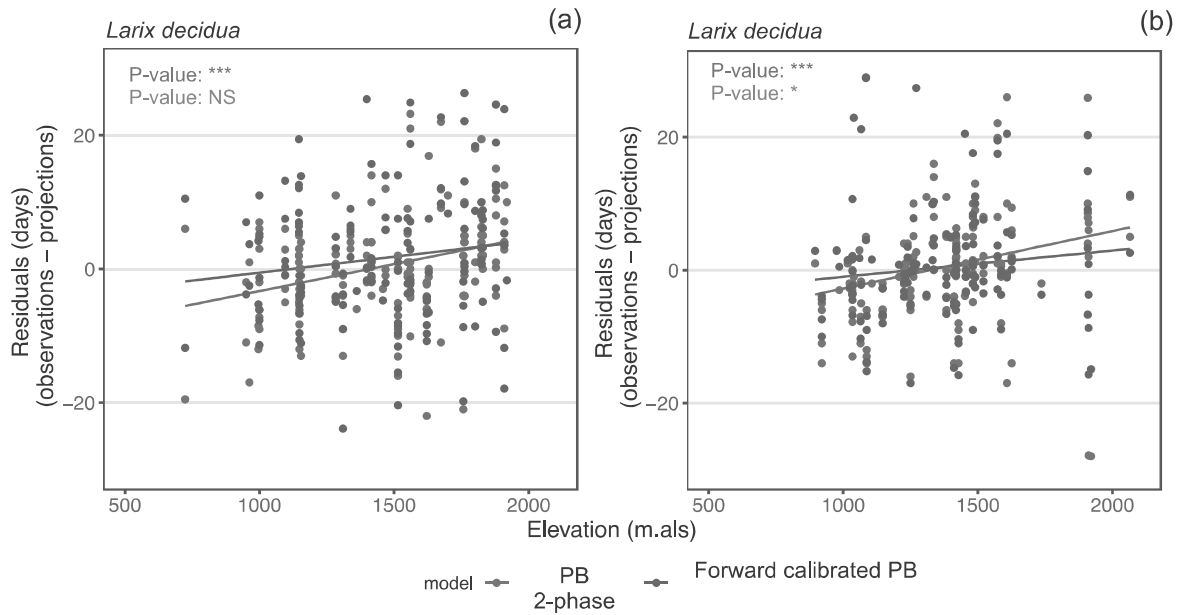
Appendix L

Comparison of the budburst dates of *Larix decidua* predicted (a) and projected (b) by the process-based 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 process-based 2-phase models (brown dots) calculated either with the calibration data subset 1 (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 Interest Statement

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:~~