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1 **Title: Representing explicit budburst and senescence processes for evergreen conifers in**
2 **global models**

3
4 **Running title:** A coniferous phenology model for global predictions

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22 **Key words:** tree phenology, needle budburst, needle senescence, evergreen needleleaves,
23 ecosystem model, RENECOFOR

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25 **Type of paper:** Primary research article

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32 **Abstract:**

33 Global ecosystem models lack an explicit representation of budburst and senescence for evergreen
34 conifers despite their primordial role in the carbon cycle. In this study we evaluated eight different
35 budburst models, combining forcing, chilling and photoperiod, for their ability to describe spring
36 budburst, and one model of needle senescence for temperate evergreen coniferous forests. The
37 models' parameters were optimized against field observations from a national forest monitoring
38 network in France. The best fitting budburst model was determined according to a new metrics
39 which accounts for both temporal and spatial variabilities of budburst events across sites. The best
40 model could reproduce observed budburst dates both at the site scale (± 5 days) and at regional scale
41 (± 12 days). We also showed that the budburst models parameterized at site scale lose some
42 predictive capability when applied at coarser spatial resolution, e.g., in grid-based simulations. The
43 selected budburst model was then coupled to a senescence function defined from needle
44 survivorship observations in order to describe the full phenology cycle of coniferous forests.
45 Implemented in the process-driven ecosystem model ORCHIDEE, this new conifer phenology
46 module represented accurately the intra and inter-annual dynamics of leaf area index at both the
47 local and regional scales when compared against MODIS remote sensing observations. A sensitivity
48 analysis showed only a small impact of the new budburst model on the timing of the seasonal cycle
49 of photosynthesis (GPP). Yet, due to the faster renewal of needles compared to the standard version
50 of ORCHIDEE, we simulated an increase in the GPP by on average 15% over France, while the
51 simulated needle turnover was doubled. Compared to 1970-2000, projections indicated an
52 advancement of the budburst date of 10.3 ± 2.8 and 12.3 ± 4.1 days in average over the period 2060-
53 2100 with the best forcing and chilling-forcing models respectively. Our study suggests that
54 including an explicit simulation of needle budburst and senescence for evergreen conifers in global
55 terrestrial ecosystem models may significantly impact future projections of carbon budgets.

56 1. Introduction

57

58 The phenology of conifers is strongly correlated with local climate (Steiner, 1980; Worrall, 1983;
59 Burr *et al.*, 1989; Leinonen & Hänninen 2002; Hänninen *et al.*, 2007). A number of previous studies
60 concluded that the growing-season length of conifer forests will extend with climate warming and
61 rising CO₂ concentration, thus leading to significant modifications of biogeochemical processes
62 being controlled by phenology (Murray *et al.*, 1994; Polgar & Primack, 2011; Gunderson *et al.*,
63 2012; Migliavacca *et al.*, 2012; Richardson *et al.*, 2013). For both deciduous and evergreen species,
64 phenology is commonly divided into three different phases: bud dormancy, bud flush and
65 senescence. The timing of these events partly controls the seasonal cycle of leaf area index and
66 gross primary productivity (GPP; Chen *et al.*, 2016). It also impacts albedo, evapotranspiration, and
67 litter inputs to the soil, of which the latter affects soil respiration (Richardson *et al.*, 2013). On
68 longer time scales, phenology also impacts the competitiveness of a species and its spatial
69 distribution (Baldocchi *et al.*, 2001; Chuine & Beaubien, 2001; Polgar & Primack, 2011). These
70 impacts make it essential to represent phenological events accurately in ecosystem models, both in
71 space and in time, if we seek to improve the simulation of the future role of vegetation in carbon,
72 water and nutrient cycling and its feedbacks on climate. Richardson *et al.* (2012) pointed out to
73 shortcomings in the representation of phenological processes in global vegetation models. Almost
74 all of the 14 vegetation models with different phenology parameterizations that they compared
75 overestimated the length of the growing season and consequently the GPP for temperate and boreal
76 forests.

77 The state of the understanding of complex molecular pathway processes of dormancy and budburst
78 mechanisms is insufficient to allow a fully mechanistic simulation in global models (Rohde &
79 Bhalerao, 2007; Yakovlev *et al.*, 2008; Rinne *et al.*, 2011; Cooke *et al.*, 2012). Thus, empirical
80 models are used for estimating the response of budburst to temperature. Several conceptual models
81 using temperature to determine the date of budburst have been proposed: they fall into two broad
82 categories. The first category assumes that budburst occurs after a threshold of degree-days has

83 been reached during a specific period (forcing). The second class of models assumes that budburst
84 requires both a chilling period during winter followed by a forcing from increasing temperature. We
85 investigated models belonging to both these categories. For conifers, photoperiod, in combination
86 with temperature, has also been proposed as a controlling variable, particularly for boreal regions
87 where the chilling requirement can be quickly reached and photoperiod acts as a safety limitation to
88 prevent a too early budburst and plant exposure to frost (Richardson *et al.*, 2013; Way and
89 Montgomery, 2015).

90 Empirical models for budburst are generally derived from local meteorological data and observed
91 budburst timing, and mostly focus on deciduous species. The direct use of a model calibrated on a
92 site for gridded simulations over a region can be a source of errors, for example because of
93 altitudinal differences not resolved at a given grid horizontal resolution or because the whole range
94 of temperatures was not taken into account during the calibration (Olsson *et al.*, 2013). This
95 problem calls for a multi-site calibration of budburst models with data drawn from a wide area,
96 typical of that used in the grid-based applications of ecosystem models.

97 Regarding the mechanisms involved, past studies did not highlight phenological differences
98 between deciduous and evergreen conifers for budburst. However, compared to deciduous species
99 that shed their leaves in autumn, evergreen conifers keep most of their needles over the year. Needle
100 lifespan can span from 2-3 years (e.g. *Pinus Sylvestris*) to more than 10 years (e.g. *Picea abies*) for
101 evergreen conifers. Needle senescence has been less studied (Estrella & Menzel, 2006; Delpierre *et*
102 *al.*, 2009) than budburst. Some authors observed a peak of senescence during autumn (Sampson *et*
103 *al.*, 2003; Kivimäenpää & Sutinen, 2007; Wang & Chen, 2012), however integrated over all needle
104 cohorts, needle senescence can be seen as a continuous process in evergreen species. Reich *et al.*
105 (2014) showed the role of needle longevity (related to nitrogen content) and the impacts of needle
106 senescence on carbon cycling in boreal forest, but very few studies investigated the regulation of
107 needle yellowing and turnover (renewal rate of needles), and none of them proposed any
108 mechanistic model for needle senescence (Muukkonen, 2005; Kayama *et al.*, 2007).

109 While current global vegetation models roughly simulate phenological events for deciduous species,
110 these processes are still lacking for evergreen species for which the common approach is to
111 represent phenology implicitly through leaf biomass variations.

112 In this study, we tackle the following objectives:

113 - To calibrate empirical budburst models for temperate needleleaved species in order to
114 reproduce field observations collected in forest monitoring plots for a range of contrasting
115 climate conditions.

116

117 - To evaluate the accuracy of these models when used at low spatial resolution (0.25 and 0.5°)
118 typical of global models and to test the simulation results against independent remote
119 sensing observations.

120

121 - To implement a model for needle senescence on the basis of litterfall observations.

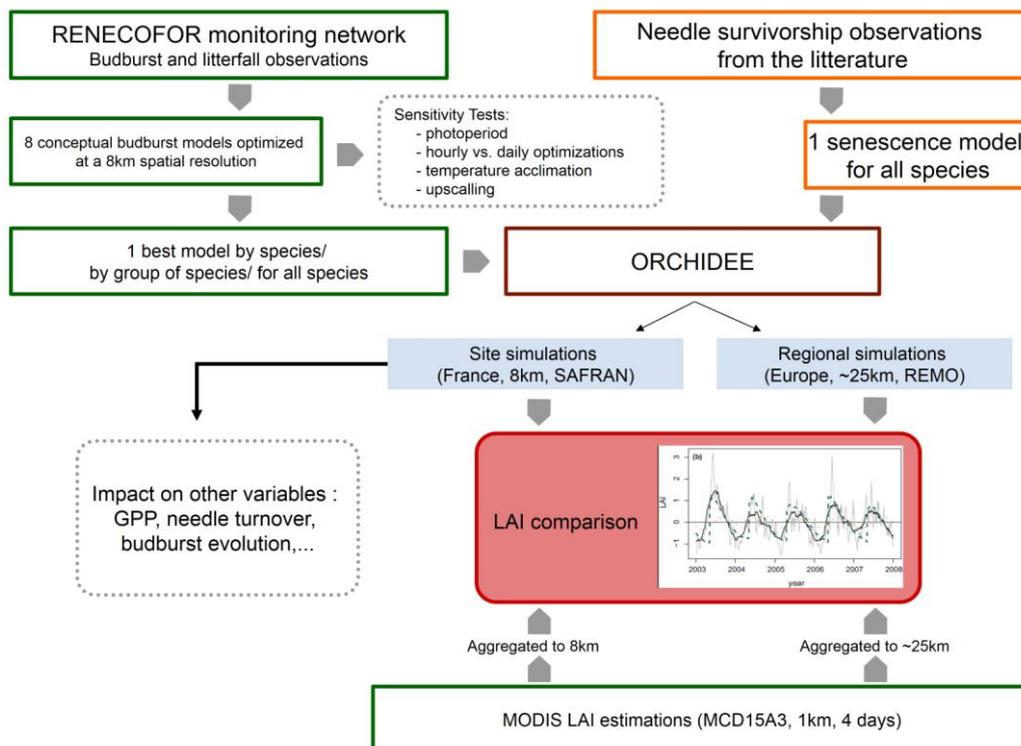
122

123 - To evaluate the potential impact of these model developments in a global vegetation model
124 (ORCHIDEE - Organizing Carbon and Hydrology In Dynamic Ecosystems; Krinner *et al.*,
125 2005) on the representation of forest canopies and the associated carbon balance simulated
126 for temperate needleleaved forests in France.

127

128 **2. Materials and methods**

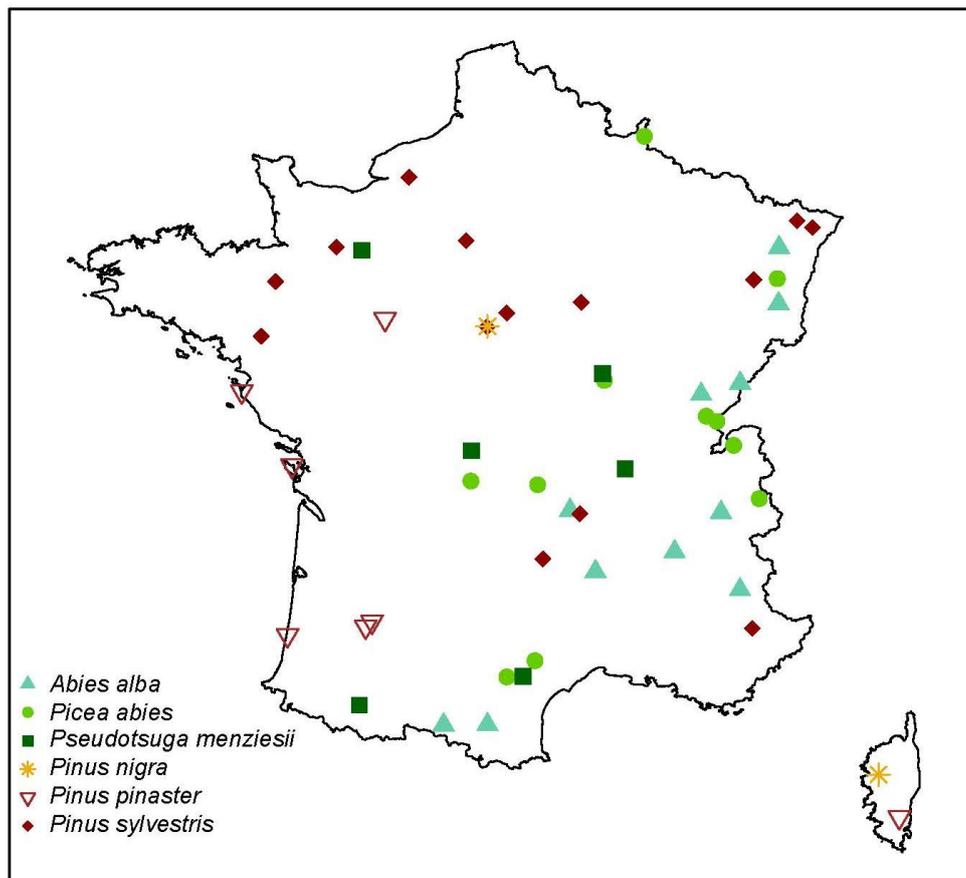
129
 130 We used budburst observations and litterfall samples collected from 1997 to 2011 over the 51 forest
 131 plots of the French RENECOFOR (REseau National de suivi à long terme des ECOsystèmes
 132 FORestiers) network covering the six main coniferous species in France (number of plots in
 133 parentheses): *Pseudotsuga mensiezii* (Douglas fir; 6), *Picea abies* (Norway spruce; 11), *Pinus nigra*
 134 (Corsican pine; 2), *Pinus pinaster* (Maritime pine; 7), *Pinus sylvestris* (Scots pine; 14) and *Abies*
 135 *alba* (Silver fir; 11). The parameters of eight different budburst models were calibrated against the
 136 RENECOFOR site observations to get the best value for a performance metrics defined specifically
 137 to account for both temporal and spatial variabilities. We selected the models that best described
 138 budburst for the temperate evergreen needleleaf plant functional type (PFT) as a whole, but also
 139 separately for each species. In addition, a new senescence model based on needle age was
 140 developed and calibrated based on a literature review of needle survivorship observations. The new
 141 phenology module (budburst+senescence) was then incorporated into the process-based model,
 142 ORCHIDEE, and evaluated spatially against leaf area index estimated from remote sensing
 143 observations. The flow chart of the model calibration and evaluation is given in Fig. 1.



144 **Fig. 1:** Flow chart of the model calibration and evaluation
 145

146
147 2.1. Data from the *RENECOFOR* forest monitoring network

148
149 Visual observations of the timing of budburst were collected in 51 plots located in public forests
150 and stratified according to the major commercial tree species grown in France. Those plots are part
151 of the French national long-term forest monitoring network (*RENECOFOR*, part of the ICP –
152 International and Co-operative Program - Forest Level II program (<http://icp-forests.net/page/level-ii>)), which covers a total of 102 permanent plots (51 coniferous) monitored since 1992 (Fig. 2).



154
155 **Fig. 2:** Distribution throughout France of the 51 *RENECOFOR* permanent plots dominated by
156 evergreen coniferous tree species.
157

158 Plots are in average 70y old (in 1994) with a range from 23 to 181y old. At each location, 36 trees
159 were chosen for phenological observations (Lebourgeois *et al.*, 2010), and observations were
160 performed at least every week. For budburst, two different dates were measured. The first one is the
161 day of the year when 10% of the trees have open buds for at least 20% of the crown (BD1). The
162 second date corresponds to the day of the year when 90% of the trees have open buds for at least

163 20% of the crown (BD9). Observations were performed each year from 1997 to 2011. We
 164 approximated a mean bud flushing date (50%; BD5) for budburst model parameterization defined
 165 as:

$$BD5 = BD1 + \frac{BD9 - BD1}{2} \quad (1)$$

166 The final dataset contains 605 site-years of observations. Litterfall was collected seasonally from
 167 1995 to 2007 at all RENECOFOR plots using litter traps. The detailed litter sampling methodology
 168 is described in the Supplementary material (Appendix SA).

169

170 2.2. Budburst models

171

172 We tested two types of model for mono-cyclical budburst events, based on a temperature forcing
 173 (e.g., degree-days) during spring, or based on “chilling-forcing”, i.e., with a chilling during winter
 174 and a forcing period during spring. We used the model M1 as reference (called the static or null
 175 model) in which budburst equals the median of the budburst dates observed across all sites (Table
 176 1). A model with predictive value (spatially or temporally) should have better performance than
 177 M1.

178

Species	Mean BD5 (SD)	Min BD5	Max BD5	n
<i>Abies alba</i>	137.5 (11.5)	109.0	175.5	148
<i>Picea abies</i>	136.8 (11.5)	107.5	169.5	132
<i>Pseudotsuga menziesii</i>	130.3 (10.9)	102.5	151.0	72
<i>Pinus nigra</i>	127.4 (14.7)	106.0	163.5	20
<i>Pinus pinaster</i>	119.6 (18.2)	81.5	164.5	77
<i>Pinus sylvestris</i>	129.5 (13.3)	97.0	175.0	156

179 **Table 1:** Mean, minimum and maximum observed budburst date (DoY) in the RENECOFOR
 180 network over the period 1997-2011. n = number of site-year observations
 181

182 Eight models (M2-M9) were taken from the literature and tested (Cannell & Smith, 1983;
 183 Hänninen, 1990; Kramer, 1994; Chuine *et al.*, 1998; Chuine, 2000; Harrington *et al.*, 2010; Vitasse
 184 *et al.*, 2011). The equations and parameters of each model are detailed in Appendix SB. All models

185 are representative of central hypotheses in budburst modeling and all of them except M9 were
 186 already applied at regional scales. The models were selected to represent different concepts, but also
 187 for their number of parameters to be small enough to allow inclusion in a global vegetation model.
 188 The list of models tested has two spring warming forcing models and six chilling-forcing models
 189 (Table 2).
 190 In addition, we performed sensitivity tests to investigate the role of photoperiod, temperature
 191 acclimation of parameters and the use of hourly or daily meteorological data (see Appendix SA for
 192 the results of the sensitivity tests).

193

	Model	Model name and reference	Number of parameters (without t_o , t_c and $t_{c,end}$)
	M1	Reference model : median value of budburst dates observed in the field	0
Spring forcing models	M2	<i>Thermal time model</i> : M2 – Kramer, 1994	1
	M3	<i>UniForc</i> : M3 – Chuine <i>et al.</i> , 1998	2
	M4	<i>Sequential model</i> : M4 – Hänninen, 1990; Kramer, 1994	5
Chilling-forcing models	M5	<i>Parallel model</i> M5 – Cannell & Smith, 1983; Kramer, 1994	6
	M6	<i>Unified model</i> M6 – Chuine, 2000	5
	M7	<i>Alternating model</i> M7 – Kramer, 1994;	2
	M8	<i>Logistic alternating model</i> M8 – Vitasse <i>et al.</i> , 2011	3
	M9	<i>Harrington model</i> M9 – Harrington <i>et al.</i> 2010	4
	Photoperiod	The daily forcing temperature calculated in models M2-M8 is weighted by the day length following Blümel & Chmielewski (2012)	+ 1

194

195 **Table 2:** Names and references of the eight budburst thermal models optimized in this study and the
 196 corresponding number of optimized parameters when the starting date for chilling (t_c), forcing (t_o)
 197 and the ending date for chilling ($t_{c,end}$) are fixed. See Appendix SB for a full description of the model
 198 parameters and their equations. Note that critical temperature thresholds are not optimized in this
 199 study but are estimated from the observed budburst dates. For example in M2 for which classical
 200 optimization studies optimized both the base temperature (T_b) and the critical forcing threshold
 201 (F_{crit}) for budburst, here only T_b is optimized, F_{crit} being the median F_{crit} simulated at each
 202 observed budburst date with M2.

203

204 2.3. *Budburst model selection criterion*

205

206 The purpose of this study being to calibrate a budburst model for regional simulations, we needed a
207 specific performance metric that characterizes the ability of this model to capture both spatial and
208 temporal budburst gradients. Most studies have used root mean square error (RMSE, Eqn 2) or
209 linear regression between simulated and observed budburst dates to select the best phenological
210 model (Vitasse *et al.*, 2011; Olsson *et al.*, 2013). We argue that two performance criteria are
211 desirable: a representation of both spatial and temporal extremes of budburst across a region, and a
212 representation with minimal systematic spatial or temporal bias. A single metric is insufficient to
213 account for these two criteria. To select the best set of parameters for each model, we thus propose a
214 combined metric accounting for three key aspects of the model: the ability to reproduce extreme
215 values, the average bias to observations and the effect of outliers. This new criterion is the
216 Euclidean distance to optima (DIST, Eqn 3) of six weighted different metrics across sites and years.
217 This new metrics maximizes model performances by catching both spatial and temporal variabilities
218 of budburst and by reducing the chance to converge to local minimum during calibration. This
219 combined metric has two components of the RMSE to limit outliers, the squared bias (BS, Eqn 4)
220 and the squared difference between standard deviation (SDSD, Eqn 5; Kobayashi & Salam, 2000)
221 normalized by the mean natural difference observed between sites $SDSD_{nat}$ and BS_{nat} ; the Spearman
222 rank correlation coefficient (R_s), the linear regression slope (lm_s ; Eqn 6) and its associated
223 coefficient of determination (lm_{R^2}) between observed and modeled budburst, which captures
224 extreme values; finally the average bias (AB, Eqn 7), and temporal and spatial biases between
225 modeled and observed budburst dates. For the purpose of large scale simulations, more weight was
226 given to capture bias and extremes than outliers (Eqn 3), with the sum of weighting factors equaling
227 1. With this metrics, the best performance is achieved when $DIST=0$. The different components of
228 DIST are:

$$RMSE = \sqrt{\frac{1}{n} \sum_{t=1}^n (x_t - y_t)^2} \quad (2)$$

$$DIST = \sqrt{\left(0.05 \left(\frac{SDSD}{SDSD_{nat}} \right)^2 + 0.05 \left(\frac{BS}{BS_{nat}} \right)^2 + 0.2(R_s - 1)^2 + 0.1(lm_s - 1)^2 \right.} \quad (3)$$

$$\left. + 0.1(lm_{R2} - 1)^2 + 0.5AB^2 \right)$$

$$BS = (\bar{x} - \bar{y})^2 \quad (4)$$

$$SDSD = (SD_x - SD_y)^2 \quad (5)$$

$$y = cste + lm_s x \quad (6)$$

$$AB = \frac{1}{n} \sum_{t=1}^n \frac{(y_t - x_t)}{x_t} \quad (7)$$

229

230 with x and y the observed and simulated budburst date, n the number of observations t , and SD the
 231 standard deviation.

232 $SDSD_{nat}$ and BS_{nat} were defined as the SDSD between sites in similar conditions and represent
 233 variability in the observed data. Pairs of sites being within 0.5° (~55 km) maximum distance, with a
 234 mean annual temperature difference less than 0.5°C , are considered as having “similar conditions”.
 235 Here, species similarity was not specified as a “similar condition”, in order to have enough
 236 observations. Thus, we hypothesized that $SDSD_{nat}$ and BS_{nat} are caused by species differences but
 237 also non-resolved biotic or edaphic factors (local adaptation, age, soil effect, etc...), and define the
 238 smallest value that an optimized model should approach when considering all conifers species. The
 239 $RMSE_{nat}$ was estimated from nine sites with “similar conditions” to 7.6 ± 3.5 days, $SDSD_{nat}$ to
 240 3.16 ± 5.09 days² and BS_{nat} to 41.76 ± 38.46 days².

241 The optimization of the parameters of models based on cross-site spatial variability only (DIST-S
 242 averaging budburst years across site) resulted in a different best model to the one based on the
 243 temporal variability only (DIST-T averaging budburst dates across all the sites each year) or
 244 considering both the spatial and temporal variability (DIST-ST). Thus, we optimized below the
 245 parameters of the eight budburst models described in Table 2 and we selected as “best predictive

246 model” the one corresponding to the minimum value of the DIST-ST metrics.

247

248 2.4. Budburst model optimization

249

250 The parameters of each model were optimized to minimize the value of DIST-ST against a subset of
251 the RENECOFOR observations (optimization dataset) consisting of 455 sites-years randomly
252 selected from the full dataset, with at least one observation per site. The remaining 150 observations
253 were used as cross-validation data. Note that models have different numbers of parameters (Table
254 2), i.e., different degrees of freedom. In addition to the cross-validation, the overall model accuracy
255 was assessed by coupling DIST-ST results to the Akaike’s information criterion corrected for
256 sample size (AICc) in order to select the best predictive (DIST-ST) and parsimonious (AICc)
257 model. Parsimonious models were selected by calculating the AICc difference (ΔAIC) between
258 AICc and the minimal AICc obtained among all models. Thus, the higher is ΔAIC , the less
259 parsimonious is a model. Models with ΔAIC higher than 10 were excluded (Burnham & Anderson,
260 2003).

261 We optimized models with a generalized simulated annealing algorithm (R package genSA;
262 Chuine, 2000; Xiang *et al.*, 2013) considering parameters 1) per species, 2) grouping pines (*Pinus*
263 *pinaster*, *Pinus sylvestris* and *Pinus nigra*) versus firs and spruces (grouping *Abies alba*, *Picea*
264 *abies* and *Pseudotsuga mensiezii*, hereafter ‘fir’) into two groups according to Peaucelle *et al.*
265 (2016), and 3) pooling all conifer species together. Models were also fitted site by site to assess
266 possible emerging relationships between local parameter values and environmental conditions
267 (Appendix SA). For chilling-forcing models (M6-M9), an exponential relationship between chilling
268 units and forcing units is commonly used to estimate budburst. However, this exponential
269 relationship is potentially an artifact (Chuine, 2000) and is not observed for all species. We thus
270 decided to compare relationships fitted by exponential or by linear functions (Appendices SA &
271 SB). Different optimizations were performed by fixing or by optimizing the starting date of forcing
272 (t_o ; 1st of January) and chilling (t_c ; 1st of November) in order to assess the models’ robustness with

273 fewer degrees of freedom. For M6 to M8 we assessed the impact of optimizing the end date for
274 chilling accumulation ($t_{c,end}$), thus representing the fulfillment of the chilling requirement, otherwise
275 chilling is summed until budburst (Vitasse *et al.* 2011).

276

277 2.5. Meteorological dataset

278

279 We used the SAFRAN (Système d'Analyse Fournissant des Renseignements Adaptés à la
280 Nivologie) meteorological data (Vidal *et al.*, 2010) for model optimization and for ORCHIDEE
281 site-scale simulations. This dataset produced by the Centre National de Recherches
282 Météorologiques (CNRM) provides hourly weather data over France at a spatial resolution of 0.07°
283 (8 km). At 0.07° resolution, each of the 51 coniferous forest sites is located in an independent grid
284 cell. Once the best set of parameters was retrieved for each model, we assessed the effect of the
285 spatial scale of climate data by applying the same models with SAFRAN data aggregated at 0.25°
286 ($\sim 28\text{ km}$) and 0.5° ($\sim 55\text{ km}$) resolution respectively. At 0.25° resolution, 49 grid cells contained at
287 least one site, and at 0.5° , 43 grid cells contained at least one site. All temperatures were corrected
288 in a simple way for local altitude following Eqn 8 (U.S. Standard Atmosphere, 1976, Olsson &
289 Jönsson, 2015):

$$T_{obs} = T_{saf} + 6.4(A_{saf} - A_{obs}) \quad (8)$$

290 where T_{obs} ($^\circ\text{C}$) is the mean observed temperature of the site, T_{saf} ($^\circ\text{C}$) the mean temperature of the
291 site from SAFRAN dataset, A_{saf} (km) the mean altitude of the SAFRAN cell and A_{obs} (km) the
292 altitude of the site.

293

294 2.6. Senescence model

295

296 The senescence model is not a stand-alone model as is the case for the model of budburst dates, but
297 rather a modification of the ORCHIDEE original phenology described in Krinner *et al.* (2005).
298 Compared to budburst models that are functions of environmental conditions, the senescence model

299 is based on needle age. The original version of ORCHIDEE includes two types of senescence for
300 needles. Firstly, a base rate of leaf mortality is applied each day (Krinner *et al.*, 2005). It represents
301 the probability for needles to fall independently of needle age or meteorological conditions.
302 Secondly, senescence is triggered when needle age (calculated for four cohorts as in Section A1 of
303 Krinner *et al.*, 2005) reaches a pre-defined longevity parameter for each PFT. As no phenological
304 process is explicitly defined in the default model, needle age is implicitly estimated from needle
305 biomass with the assumption that newly assimilated biomass through photosynthesis is used to
306 create new needles at the beginning of the year.

307 We did not find any suitable needle senescence model for coniferous species in the literature. We
308 thus decided to fit a senescence function against field observations of needle survival probability
309 from different studies (all studies and species are listed in Table SC1, Appendix SC). We retrieved
310 45 needle survivorship curves (determines the probability of needles to survive (0-1) over time
311 according to their age) from the literature and used these to calibrate a logistic function given by:

$$S(t) = \frac{1}{1 + e^{(4\mu(\lambda-t)+2)}} \quad (9)$$

312 Where $S(t)$ is the survivorship probability of a needle, t the needle age (days), and μ (days^{-1}) and λ
313 (days) parameters to be fitted on literature observations.

314

315 2.7. Modification of the ORCHIDEE model

316 The inclusion of an explicit phenology for evergreen conifers in ORCHIDEE (Krinner *et al.* 2005)
317 needed the modification of the original model. The needle maximum age parameter for evergreen
318 conifers, fixed at 910 days (average lifespan of *Pinus* needles) in the standard version of
319 ORCHIDEE was modified to depend on species. This maximum age can vary considerably, going
320 from 2 years in pine species to more than 10 years for *Abies alba* and *Picea abies* (Peaucelle *et al.*,
321 2016). In ORCHIDEE, the V_{cmax} parameter (maximal rate of the RUBISCO carboxylation activity
322 in $\mu\text{mol m}^{-2} \text{s}^{-1}$) increases with needle age, reaching a maximum value when the relative age of the
323 needle (the ratio of the needle age to its maximum) is 0.03 and then linearly decreasing to its

324 minimum value when the relative age reaches 0.5. This function describing the evolution of V_{cmax}
325 roughly represents species with short-lived needles such as pines (Niinemets, 2002). Observations
326 show a rapid decrease of V_{cmax} after only 1 year even in high needle-longevity species (Porté &
327 Loustau, 1998; Niinemets, 2002; Warren, 2006). We thus adapted this relationship prescribing V_{cmax}
328 to reach its maximum 3 months after formation and then starting to decrease linearly after one year,
329 until reaching $0.5 V_{cmax}$ at the maximal needle age of the species. In following simulations, we used
330 two different needle maximum age, 1275 and 2340 days for pines and spruces/firs species,
331 respectively (Peaucelle *et al.*, 2016).

332 Given the senescence function in Eqn 9, we also modified the way carbon is distributed in the
333 crown by representing each cohort of needle (*i.e.* groups of needles developed the same year). All
334 the biomass gained during the current year is placed in the youngest needle cohort. Other cohorts do
335 not receive new biomass, but lose needles according to the senescence function from Eqn 9. To
336 exclude simulations where budburst never occurs, we imposed a maximum needle onset at day 182
337 (1 July), the latest observed budburst in our dataset.

338

339 2.8. Validation of the phenology models

340

341 Simulated budburst date was evaluated against observed data from the optimization and the cross-
342 validation dataset. We also investigated the ability of each model to predict spatial and temporal
343 variations in budburst across sites by comparing median modeled and observed budburst dates at
344 each site, and by looking at the interannual variability in the timing of budburst at each site.

345 Because of the high cross-site variability, an evaluation of the senescence model could not be
346 performed against litterfall observations, which also depend on non-modeled factors such as stand
347 health, stand age, density, species composition and management events. Thus, observed and
348 modeled litterfall were simply compared for information, and we validated the senescence model
349 through the indirect comparison with satellite-derived leaf area index (Wang *et al.*, 2004). We
350 compared LAI simulated at a spatial resolution of 0.07° with ORCHIDEE forced by SAFRAN

351 against MODIS MCD15A3 LAI (1 km, 4-day frequency; Myneni *et al.*, 2002). This local
352 comparison between modeled and satellite LAI was performed on a few grid cells where the
353 coverage of two representative coniferous species (*Picea abies* and *Pinus sylvestris*) exceeds 80% at
354 1 km, based on the European tree species map of Brus *et al.* (2012). The correlation coefficient
355 between modeled and estimated LAI was used to assess modeled LAI seasonality.

356 We also performed grid-based simulations for coniferous forests in Europe at a 0.25° spatial
357 resolution to compare simulated and satellite LAI at a larger scale over the period 2000-2007. Initial
358 conditions and forcing data used for simulations are detailed in the Supplementary Material
359 (Appendix SA).

360 Finally, we ran the model over France at a resolution of 0.07° for the period 1970-2100 to assess
361 patterns in budburst timing in future decades. The climate forcing (daily data) was from the A2
362 scenario of ARPEGE v4 model downscaled and bias corrected by Pagé *et al.* (2008). In these
363 simulations of the future, land cover was imposed from the IGBP map (Loveland & Belward, 1997)
364 and soil depth and texture (used to derive wilting points and field capacities and thence to give plant
365 water stress) from the FAO dataset (Vetter *et al.*, 2008).

366

367 3. Results

368 3.1. RENECOFOR budburst and litterfall observations

369 On average 50% of buds flushed for the sites of Fig. 2 within a range of 14 days around the 12 May
370 (day 132; Table 1). The earliest budburst was recorded on 22 March 2007 for *Pinus pinaster* in “Les
371 Landes” forest, in southwest France. The latest budburst dates were observed in mountainous
372 regions for *Abies alba* and *Pinus sylvestris*, 24 June 1999 and 24 June 2008, respectively. On
373 average, coniferous stands dropped 2336.5 kg ha⁻¹ yr⁻¹ (dry matter) of their needles as litter from
374 1997 to 2007, which represents 65% of the total annual litterfall for all compartments on average
375 (all stands, only considering the dominant species; 49% considering secondary species) and more
376 than 70% for *Abies alba*, *Picea abies* and *Pinus pinaster* (Table 3). We could see large differences

377 in the mass of needles lost per year among species. Species with minimum losses were *Abies alba*
 378 (mean over all sites was 1892.0 kg ha⁻¹ yr⁻¹) and *Pinus sylvestris* (1859.5 kg ha⁻¹ yr⁻¹) whereas the
 379 maximum was observed for *Pinus pinaster* (3175.4 kg ha⁻¹ yr⁻¹).

380

Species	Leaves kg ha ⁻¹ yr ⁻¹	CV _L %	Prop. %	Total kg ha ⁻¹ yr ⁻¹	CV _T %	n
<i>A.alb</i>	1892.2	37.2	58.0	3263.2	33.0	145
<i>P.abi</i>	2692.6	30.6	72.8	3698.6	30.0	121
<i>P.men</i>	2036.7	31.8	84.5	2411.3	30.4	66
<i>P.neg</i>	2447.2	24.3	51.6	4740.4	18.4	21
<i>P.pin</i>	3175.4	30.3	76.1	4172.4	28.0	81
<i>P.syl</i>	1859.5	34.6	49.6	3750.4	30.0	171
All	2336.5	20.4	49.2	3580.4	21.4	605

381

382 **Table 3:** Litterfall mass (kg dry matter ha⁻¹ yr⁻¹) measured in the RENECOFOR network over the
 383 period 1997-2007 for each compartment. CV corresponds to the coefficient of variation for each
 384 compartment (leaves, and total) and Prop. corresponds to the proportion of the compartment
 385 compared to the total litterfall. P.men=*Pseudotsuga menziesii*, P.abi=*Picea abies*, P.neg=*Pinus*
 386 *negra*, P.pin=*Pinus pinaster*, P.syl=*Pinus sylvestris*, A.alb=*Abies alba*.

387

388 3.2. Budburst models comparison and selection of a best model

389 Best models (parsimonious and predictive) retained for each species are listed in Table 4 and the
 390 corresponding model parameters are given in Table SC2 (Appendix SC). Figure SC1 shows the
 391 DIST-ST evaluation metric after parameter optimization for each model forced by daily
 392 temperatures. For all species together, the best model (DIST-ST criterion) is the simple spring
 393 forcing model M3 (DIST-ST=0.25, RMSE=12.5 days, Fig. 3) with a starting date fixed to 1
 394 January. The most parsimonious is the chilling-forcing model M7 (DIST-ST=0.39). With M3, both
 395 spatial (DIST-S=0.32, RMSE=10.7 days) and temporal (DIST-T=0.17, RMSE=7.3 days) variability
 396 was well reproduced for the validation dataset. The DIST-ST values obtained with models M2, M6,
 397 M7, M8 and M9 are close to this best model, with DIST-ST of 0.35, 0.26, 0.39, 0.4 and 0.29,
 398 respectively, but only models M7, M8 and M9 are considered parsimonious according to ΔAIC.
 399 The sequential (M4) and parallel models (M5) could not reproduce observations properly (DIST-
 400 ST=1.58 to 2.56, RMSE=19.0 to 28.0 days).

401

Species	Model	DIST-ST
All	M3	0.25
Firs	M7	0.47
Pines	M7	0.46
<i>Abies alba</i>	M3	0.56
<i>Picea abies</i>	M7	1.25
<i>Pseudotsuga mensiezii</i>	M9	0.32
<i>Pinus pinaster</i>	M3	1.15
<i>Pinus sylvestris</i>	M7	0.45

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Table 4: Best models retained for each species according to both the predictive power considering spatial and temporal variability (DIST-ST) and the parsimony (with the lowest number of parameters). Models were optimized against daily temperatures. See Appendix SB for a detailed description of each model.

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For groups of species, in the case of firs, the best model is the chilling-forcing model M7 (DIST-ST=0.47, RMSE=11.9 days). The temporal variability (DIST-T=0.45) representation was equivalent to the spatial variability for M7 for firs (DIST-S=0.48). Models M2, M3, M6, M8 and M9 have performances close to M7 but only M3, M7 and M8 have a $\Delta AIC < 10$. For pines, all optimized models produced better DIST-ST values than the null model M1, but higher RMSE. The best model for pines is again the chilling-forcing model M7 (DIST-ST=0.46, RMSE=16.3 days), while the best parsimonious is M2 (DIST-ST=0.63). Model M7 better represented the spatial pattern of observed budburst (DIST-S=0.20, RMSE=10.2 days) than for temporal variability (DIST_T=0.62, RMSE=13.5 days).

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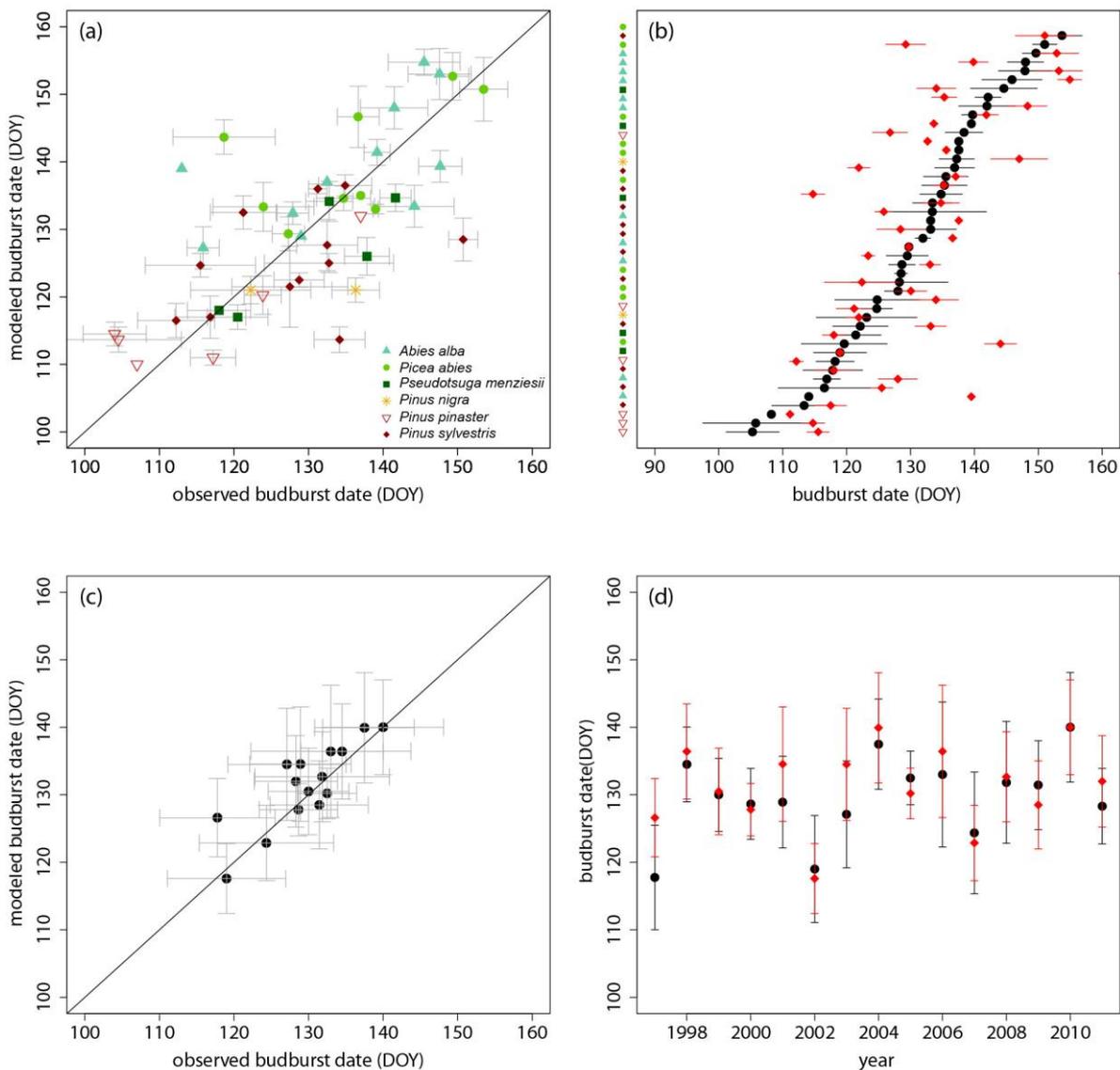
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423

For individual species, the most parsimonious model is also M7. In the case of *Abies alba* the best DIST-ST is obtained with M6 (DIST-ST=0.48) while the best parsimonious model is the model M3 (DIST-ST=0.56). For *Picea abies*, none of the models reproduced accurately the observations, M7 having the best score and parsimony with DIST-ST=1.25 (RMSE=21.0 days). For *Pseudotsuga mensiezii* the best model was M9 (DIST-ST=0.32, RMSE=10.7 days), which concurs with the results of Harrington et al. (2010) for this species. However, for both *Pseudotsuga mensiezii* and

424 *Pinus pinaster* the most parsimonious model led to high DIST-ST values, with 2.19 and 2.64
 425 respectively. For *Pinus pinaster*, the best DIST-ST was obtained with M8 (DIST-ST=0.33,
 426 RMSE=14.0 days), but was not selected as parsimonious. The best model was thus M3 with DIST-
 427 ST=1.15. Finally, the best DIST-ST for *Pinus sylvestris* was obtained with M4 (DIST-ST=0.38,
 428 RMSE=12.0 days) while the most parsimonious model is again M7.
 429 Lower performances of the optimization at the species level compared to groups of species can be
 430 explained by the smaller training dataset available for parameter calibration. We argue that models
 431 calibrated with all species or groups of species should thus be more robust and more suitable for
 432 large scale simulations.
 433



434

435 **Fig. 3:** Results for each site and each year for the best model with all species together (model M3).
436 Representation of the validation dataset (150 obs.). (a) and (b) correspond to mean dates by site
437 (Error bars correspond to the inter-annual variability), (c) and (d) correspond to mean dates by year
438 (all sites together, error bars correspond to the inter-site variability). The y-axis of (b) represents
439 each site for which the dominant species is represented by symbols listed in (a). For (b) and (d),
440 black dots correspond to mean observations, red diamonds correspond to mean modeled budburst
441 dates.
442

443 Results with or without optimizing the starting date for temperature accumulation (t_o , t_c) have
444 similar model performance (Fig. SC1). However, we can see different performances of the same
445 model depending on the species. For example, the optimization of model M6 with fixed t_c led to
446 better DIST-ST for *Picea abies* and worse DIST-ST for *Pseudotsuga mensiezii* compared to M6
447 with optimized t_c . Thus, we preferentially selected models with a fixed starting date for large scale
448 simulations when optimization results were equivalent. The same conclusion applies to
449 optimizations with varying t_{cend} (end of chilling accumulation).
450

451 For all species, pines and firs, we found quiet similar performances for both forcing and chilling-
452 forcing models. Note that chilling-forcing models may still be more physiologically realistic for
453 future predictions where warmer winters may exacerbate the effects of incomplete fulfillment of
454 chilling, or for applications in cold regions where chilling should be more important than in France
455 and western Europe. We selected M3 (forcing) and M7 (chilling-forcing) for inclusion in
456 ORCHIDEE.

457

458 3.3. Model performances from site-scale to grid-based resolution

459

460 We checked for model robustness at lower spatial resolutions, representative of typical forcing data
461 for global vegetation models. At 0.25° resolution, most of DIST-ST values were higher than at a
462 resolution of 0.07° and the best models differed. For all species, the best DIST-ST increased from
463 0.25 (M3- t_o) to 0.43 (M8+ t_o+t_c). But the best parsimonious model was still M7 with a DIST-ST
464 value of 0.49. Some models were no longer able to work correctly and DIST-ST values diverged

465 (DIST-ST= 132.2 for *Pinus sylvestris*-M8). At 0.5° the most parsimonious model remained M7 but
466 DIST-ST increased from 0.49 to 0.77. If we compare the evolution for the best models M3 and M7
467 at 0.07° and 0.5°, we can observe that the result is more degraded for M3 (DIST-ST increased from
468 0.25 to 1.77) than for M7 (DIST-ST from 0.39 to 0.77), but is still a much better performance than
469 the null model M1 with DIST-ST=9.17.

470 At a lower spatial resolution, some models could not be used. This was the case for models with a
471 fixed threshold for chilling accumulation (M4, M5 and M6). By averaging temperatures, the critical
472 threshold for chilling accumulation of these models was never reached at some sites and
473 consequently forcing temperatures could never accumulate. In the rare cases when the model
474 succeeded in estimating a budburst date, we could see that the performance was lower than the null
475 model M1 (DIST>10). The implications of using models derived at the site scale for low-resolution
476 prediction are further addressed in the discussion section.

477 478 3.4. *Senescence model parameters*

479
480 The minimum and maximum needle lifespan in Eq. 9 retrieved from literature studies were 4 and 15
481 years, respectively. Independently of environmental factors, species or tree health, needle
482 survivorship follows almost the same pattern in each study: the needle biomass turnover is
483 relatively low during the first years of the needle life and then rapidly increases over time. The
484 logistic relationship we fitted on those data was strongly correlated to the needle lifespan of the tree
485 (Eqn 10, Eqn 11) with $R^2=0.93$ and 0.94 for parameters μ and λ , respectively (Fig. SC3, SC4;
486 Appendix SC).

$$487 \ln(\mu) = 1.35 - 1.33\ln(Needle_{age}); R^2 = 0.93 \quad (10)$$

$$488 \lambda = -0.82 + 0.43Needle_{age}; R^2 = 0.94 \quad (11)$$

487 with $Needle_{age}$ the maximal needle age.

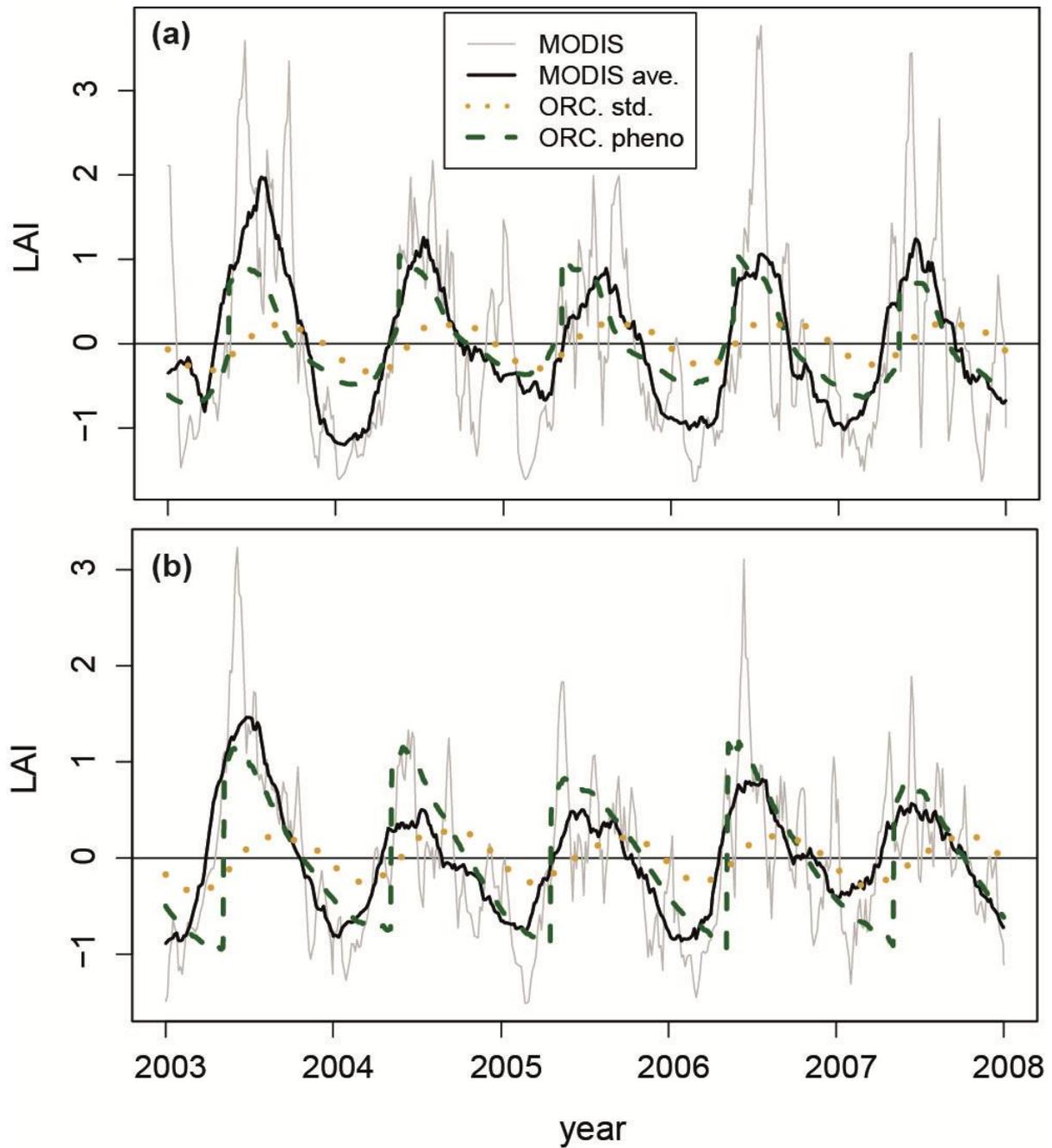
488 The strong correlation between senescence parameters and the maximal needle age thus allows the
489 use of one unique relationship for all species.

490

491 3.5. Comparison against satellite data

492

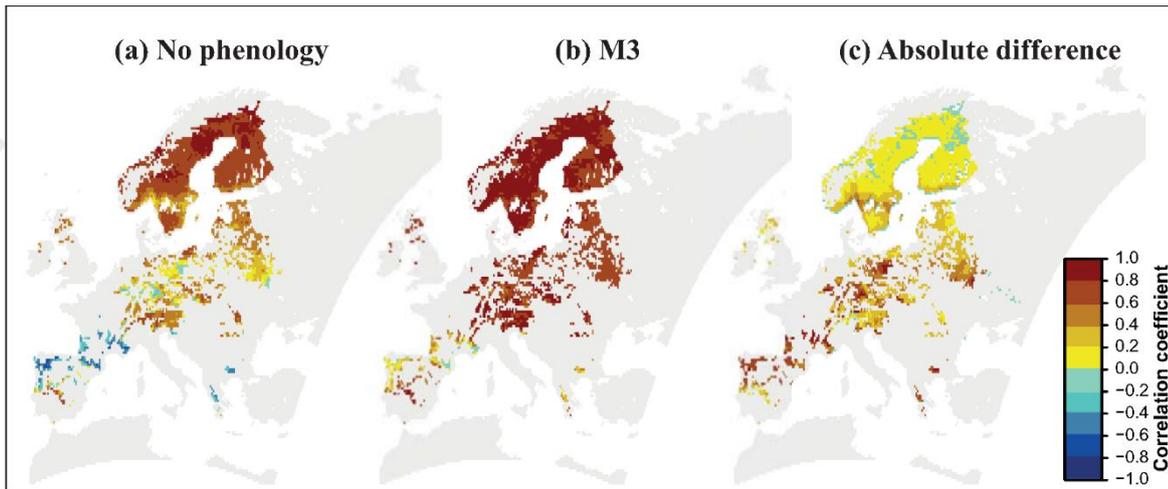
493 We first compared LAI simulated at site scale for two representative species (*Picea abies* (Fig. 4a)
494 and *Pinus sylvestris* (Fig. 4b)) with MODIS satellite observations over the MODIS pixel of 1 km
495 containing each site. Simulations were performed here with budburst results obtained for the pines
496 and fir/spruces groups. For both models M3 (best forcing model) and M7 (best chilling-forcing
497 model), results are equivalent. The amplitude of the LAI cycle with the improved phenology
498 (1.4 ± 0.1 for *Pinus sylvestris*; 1.2 ± 0.1 for *Picea abies* - model M7) was closer to the amplitude of
499 observed LAI (1.7 ± 0.6 ; 1.9 ± 0.7) than with the standard version of the model which does not have
500 an explicit needle budburst equation (0.4 ± 0.1 ; 0.4 ± 0.1 , respectively). For the 15 sites compared
501 with MODIS LAI for each species, the mean correlation coefficient between modeled and estimated
502 LAI improved from 0.45 ± 0.2 to 0.77 ± 0.1 for *Picea abies* and from 0.47 ± 0.2 to 0.71 ± 0.1 for *Pinus*
503 *sylvestris*.



504
 505 **Fig. 4:** Comparison between observed (MODIS) and simulated (model M7) LAI dynamics with
 506 ORCHIDEE for a) a *Picea abies* stand (lat=50.16°, long=5.46°) and b) a *Pinus sylvestris*
 507 stand (lat=49.25°, long=8.06°). All data are centered on the average observed (or simulated) LAI value
 508 (2003-2008). Gray and black lines represent the observed MODIS LAI and the moving average
 509 over a 30-days window, respectively. The orange dotted line represents the simulated LAI with the
 510 standard version of ORCHIDEE without phenological processes. The green dashed line represents
 511 the simulated LAI with ORCHIDEE including budburst and senescence processes.
 512

513 Figure 5 shows the correlation coefficient between satellite-observed and simulated LAI at the
 514 European scale with the best forcing model (M3 optimized with all species) and the senescence
 515 model. The spatial correlation between modeled and satellite LAI improved by 0.24 (from

516 $R=0.48\pm0.3$ to 0.72 ± 0.2) over Europe even if the calibration was performed only over France. We
 517 could observe the same improvement with the best parsimonious chilling-forcing model M7
 518 ($R=0.69\pm2$). Moreover, we observed that the modeled budburst with M3 reached the imposed limit
 519 of budburst date in very high latitudes and altitudes. On the contrary, the chilling-forcing model M7
 520 was better able to predict the LAI seasonality at high altitudes and high latitude, because it never
 521 reached the imposed budburst date in these areas.



522 **Fig. 5:** Spatial representation of the correlation coefficient between MODIS estimated LAI and
 523 ORCHIDEE simulated LAI at a 0.25° spatial resolution averaged over the period 2000-2007: a) in
 524 the standard configuration without explicit phenological processes, or b) with the budburst model
 525 M3 and the senescence model. Map c) gives the absolute difference (b - a). Only the dominant
 526 species used in this study are represented (*Abies alba*, *Picea abies*, *Pinus pinaster*, *Pinus sylvestris*,
 527 *Pseudotsuga mensiezii*). The correlation is calculated for pixels with a minimal coniferous fraction
 528 cover of 20%.
 529

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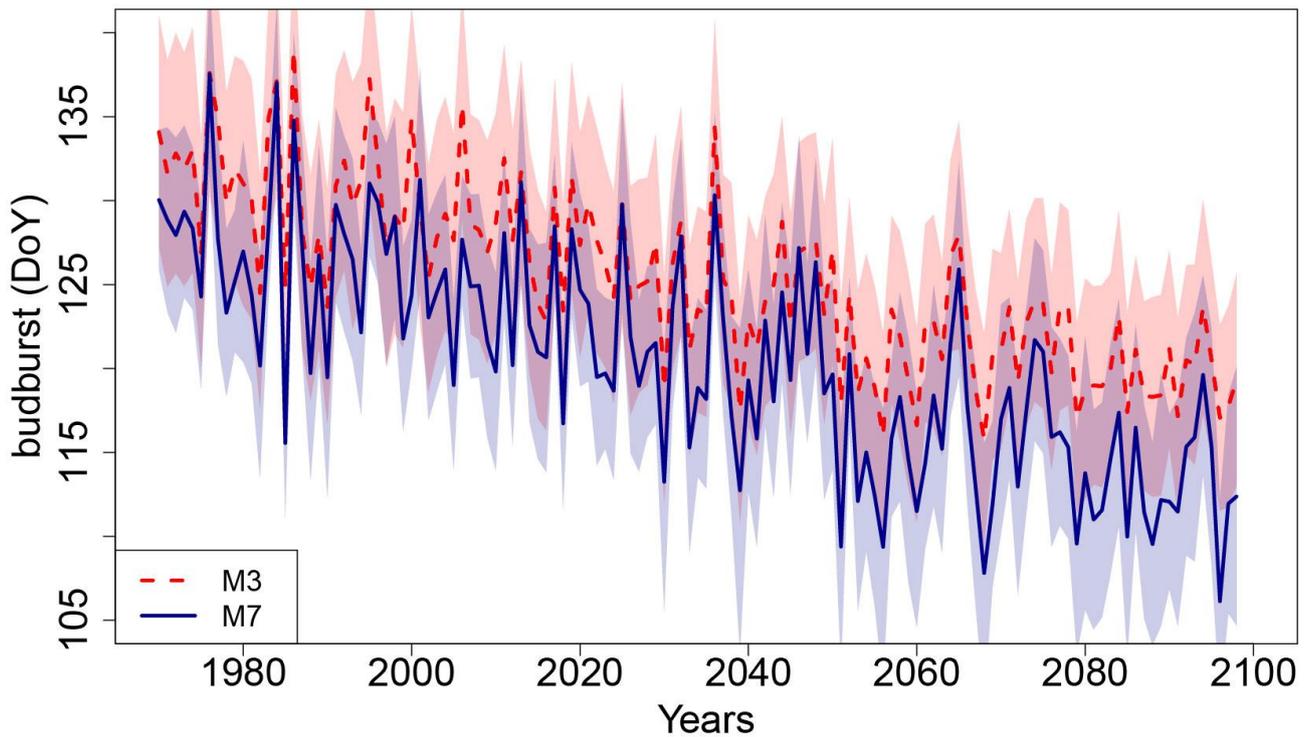
532

533 3.6. Budburst evolution from 1970 to 2100

534

535 Figure 6 shows the simulated evolution of the mean budburst date over France from 1970 to 2100
 536 with the best model M3 and the most parsimonious forcing-chilling model M7. For the two models,
 537 we simulated an earlier needle unfolding over time (mean slope= -0.126 ± 0.01 days yr^{-1} , R^2
 538 $=0.57\pm0.06$). Compared to 1970-2000, projections indicated an advancement of the budburst date of
 539 coniferous species of 10.3 ± 2.8 and 12.3 ± 4.1 days in average over the period 2060-2100 with M3
 540 and M7, respectively. However, model M7 exhibited higher variability in the prediction of needle
 541 unfolding over time and an earlier budburst date on average compared to M3 (4.8 ± 0.8 days) over

542 the period 1970-2100.



543
544 **Fig. 6** : Temporal evolution of the mean budburst dates (DOY) simulated over France from 1970 to
545 2100 for models M3 and M7 (all species together). For each line, the corresponding colored area
546 indicates one s.d. either side of the mean.
547

548

549 3.7. Impact of the new conifer phenology model on GPP

550 We assessed the impact of the new phenology model on the simulated GPP. We found in our
551 simulations an increase of GPP by $15 \pm 1\%$ when compared to the standard version of ORCHIDEE.
552 For example, GPP increased from an average $5.5 \pm 0.2 \text{ g C m}^{-2} \text{ d}^{-1}$ to $6.3 \pm 0.2 \text{ g C m}^{-2} \text{ d}^{-1}$ for spruce
553 stands over France during the historical period (2000-2010). GPP increase was mainly induced by a
554 modification of the canopy composition. Due to the production of new needles each year and
555 senescence removing old needles, needle cohorts forming the canopy are younger (see Materials
556 and methods) in the new model (845.3 ± 55.5 days for spruces versus 1740 ± 18.8 days in the standard
557 version of ORCHIDEE). New needles having higher photosynthetic rates, this results into a higher
558 simulated GPP. Because old needles are already present at the beginning of the growing season (i.e.
559 photosynthetic activity starts as soon as climate conditions are favorable) and because new needles

560 reach their maximal activity only 3 months after unfolding, simulated GPP was not sensitive to
561 changes in budburst date. By imposing the needle onset (from day 90 to 160), we observed a mean
562 GPP difference of $0.002 \text{ g C m}^{-2} \text{ d}^{-1}$, which sums up to only $0.8 \pm 0.1 \text{ g C m}^{-2}$ over the whole year
563 for each day difference in budburst.

564 With the new senescence model instead of the standard parameterization, we found an increase of
565 the needle turnover from 0.16 ± 0.002 to $0.43 \pm 0.025 \text{ g C m}^{-2} \text{ d}^{-1}$ for spruce. Consequently, litterfall
566 for *Picea abies* stands without explicit senescence has an average of $1155.0 \pm 12.6 \text{ kg ha}^{-1} \text{ yr}^{-1}$ over
567 France while we simulated losses of $3146.5 \pm 182.7 \text{ kg ha}^{-1} \text{ yr}^{-1}$ with explicit senescence, which is
568 closer to observations for this species ($2692.6 \text{ kg ha}^{-1} \text{ yr}^{-1}$); this is a relative difference of -57% and
569 +17%, respectively, between observed and simulated litterfalls.

570

571 4. Discussion

572

573 4.1. Uncertainties in model validation

574

575 Phenology is a central function in stands of conifers. In this study we optimized different
576 phenological models against *in situ* budburst observations for six coniferous species. We showed
577 that most models reproduced budburst dates with a precision of ± 12 days across France. However
578 we highlighted the need to consider both spatial and temporal variability when calibrating a
579 phenological model. Figure SC5 (Appendix SC) illustrates the differences in results for the two
580 spring forcing models M2 and M3 considering either the simple RMSE or our more comprehensive
581 DIST metrics to select the best model after calibration. With the model M2 the best optimization
582 based on RMSE does not allow to simulate budburst occurring before day 130 (Fig. SC5a, b), while
583 with the model M3 (Fig. SC5c, d) the best optimization based on RMSE resulted in a high
584 variability of simulated budburst. Even when considering both temporal and spatial variability of
585 budburst with the DIST metrics, our results highlighted that, while some models managed to
586 reproduce the observed budbursts (for instance M7 for firs, section 3.2), the same model calibrated

587 on different dataset generally reproduce better the spatial variability than the temporal variability of
588 budburst. The DIST metrics proposed in this study is a first attempt to take into account both
589 temporal and spatial variability of budburst. The combination of multiple metrics is promising to
590 improve model calibration but more investigation is needed to improve this metrics, like the number
591 of component we need to consider and their weight.

592 This implementation of better phenology models for evergreen conifers in the global model
593 ORCHIDEE shows an improved ability to reproduce the seasonal LAI dynamics observed from
594 MODIS both at the site and regional scale, despite representativeness differences between one site
595 and a MODIS pixel, and the contribution of understory vegetation to the MODIS signals. Previous
596 studies have shown a good correspondence between field-measured LAI and MODIS products
597 (Jensen *et al.*, 2011; Rautiainen *et al.*, 2012). However, needle senescence is locally dependent of
598 stand health, age and disturbances. We indirectly validated our senescence model against MODIS
599 LAI data, despite uncertainties of this product. Comparisons with litterfall observations further
600 allowed to show that our senescence model represent an improvement. By comparing site
601 measurements of carbon fluxes and MODIS products, Verma *et al.* (2014) highlighted the
602 uncertainties linked to the heterogeneity of the vegetation at a larger spatial resolution. In this study
603 we visually checked for canopy openness at the site scale, however LAI from MODIS products
604 integrates contributions from both the dominant species and the understory vegetation, which will
605 result in a bias when comparing PFT specific simulations and observed amplitude and dynamics of
606 the LAI (Wang *et al.*, 2004; Jensen *et al.*, 2011; Rautiainen *et al.*, 2011; Rautiainen & Heiskanen,
607 2013). Moreover, LAI is related to stand age and health (Pokorný *et al.*, 2013), which were not
608 taken into account in our study.

609 The senescence model proposed in this study defines a continuous process over the needle lifespan.
610 Moreover, we fixed the length of the period of needle accretion in ORCHIDEE, which can result in
611 biases in LAI at the beginning of the growing season. We argue that an optimization of the
612 senescence model parameters against carbon fluxes and remote sensing observations could further

613 improve the senescence model.

614

615 4.2. Relevance of site-calibrated models for gridded simulations

616

617 All tested models in this study could be optimized with good accuracy at the site scale
618 (RMSE=6.0±3.4 days for M3, 4.3±2.7 days for M7) or across sites (RMSE=12.5 days with all
619 sites). We also show that forcing models performed equally compared to chilling-forcing models at
620 the regional scale. Olsson & Jönsson (2014) indicated that simple models with few parameters are
621 more accurate over larger regions in general. In our study, most phenological models were more
622 efficient than the null model (M1), i.e., setting a fixed date equal to the median observed one, even
623 at a degraded spatial resolution. However, some models were not able to reproduce budburst events
624 when calibrated using large-scale temperature forcing data, especially models M4 and M5.

625 Modelers should be cautious when applying empirical models fitted at site scale for large-scale
626 predictions for two aspects: 1) If a model developed for site scale studies does not work at larger
627 resolutions, it means either that the model is not generic enough: the sites were too specific or some
628 processes are missing, like adaptation or acclimation for example; 2) The spatial aggregation of
629 temperatures can smooth and modify the response of chilling and forcing. Modelers have to check
630 that models calibrated on sites, and thus dependent of site conditions, are still able to reproduce
631 average responses of budburst globally and not only in limited environmental conditions. Thus the
632 model validity should be assessed at different spatial and temporal scales. The metrics developed in
633 our study lowers the weight of outliers in the calibration and thus limits this effect.

634 Here, the best forcing model M3 has more degraded performance than the best chilling-forcing
635 model M7 when applied at 0.25° and 0.5°, even if M7 exhibits a lower performance than M3 when
636 calibrated at 0.07°. This result suggests that the model M7 may be more suitable than M3 to be used
637 in a global model such as ORCHIDEE.

638 We also found that the best model calibrated with *in situ* observations is not necessarily the best
639 model to reproduce the seasonality of the satellite LAI cycle. Our results suggest that looking at the

640 whole phenological cycle, in addition to *in situ* observations, could be a better way of
641 discriminating between budburst models intended to be used in global vegetation models. In a
642 recent study, Gamon *et al.* (2016) demonstrated a method to track photosynthetic phenology in
643 evergreen conifers using a remotely sensed reflectance chlorophyll/carotenoid index (CCI). This
644 new indicator could allow an accurate calibration of phenological processes for conifers. However,
645 because of the land cover heterogeneity over Europe, a calibration of phenological models based
646 only on satellite observations would also benefit in the future from a very high temporal and spatial
647 resolution dataset (Delegido *et al.*, 2011; Verrelst *et al.*, 2012; Klosterman *et al.* 2014).

648

649 4.3. Impact of phenology for large-scale simulations of GPP and LAI

650
651 The new phenological processes incorporated into ORCHIDEE led to a better representation of the
652 seasonal cycle of LAI both at site and regional scale (Figs 5, 6). Simulated LAI was however not
653 sensitive to the timing of needle onset, while the production of new needles and the use of an
654 explicit representation of needle senescence had a strong impact on simulated variables. In our
655 simulations, all the new needle biomass was allocated to younger needles with high photosynthetic
656 efficiency, thus leading to simulated GPP being higher than in the original model. The explicit
657 representation of the senescence also led to a higher needle turnover, and litterfall. A higher
658 litterfall rate will strongly impact soil carbon pools and heterotrophic respiration. Here, the
659 estimated amount of needle-fall was in the range of values observed in French stands, while the
660 standard version of ORCHIDEE underestimated the amount of litter. However, the lack of
661 information about the living needle biomass at each site did not allow an accurate comparison of
662 simulated and observed litterfall. Needle-fall is closely related to stand age, stand health, climate
663 and disturbances (Balster & Marshall, 2000; Choi *et al.*, 2006; Reich *et al.*, 2014). The relation
664 defined in this study does not take into account all the factors influencing needle-fall and more
665 investigation is needed.

666 The strong correlation between the senescence parameters and the maximal age of needles (Eq. 7,

667 8) makes our proposed senescence model relevant for a large variety of evergreen coniferous
668 species and may be generalized to other evergreen species in other biomes. With the generalization
669 of models with varying traits (Pavlick *et al.*, 2012, Verheijen *et al.*, 2015), we argue that our
670 senescence model could be easily implemented with trade-offs concerning the maximal age of
671 needles, as for example relationships between the needle lifespan and mean annual temperatures,
672 recently implemented in the CABLE model by Reich *et al.* (2014). As for budburst, we can expect a
673 change in the senescence rate with global changes. The inclusions of trade-offs between needle
674 longevity and climate in the ORCHIDEE model as it was done by Reich *et al.* (2014) will be a first
675 step in understanding the impact of such changes on the carbon balance of forest ecosystems.
676 For evergreen species, a significant amount of leaves/needles is already present at the beginning of
677 spring. The presence of old needles thus allows the recovery of carbon and water fluxes when
678 temperatures become favorable — this explains the low sensitivity of simulated fluxes to budburst
679 date. However, even if the needle onset had few impacts in this study, the implementation of an
680 explicit budburst model was shown to play a key role in other mechanisms such as ozone sensitivity
681 of needles (Watanabe *et al.* 2010; Verbeke, 2015), frost risk (Hänninen, 2006; Man *et al.*, 2015),
682 biogenic emissions (Richardson *et al.*, 2013) or vegetation dynamics (Lu *et al.*, 2016). The
683 mechanisms presented in this study could be extended to improve the representation of other
684 evergreen species in global models.

685 **5. Conclusion**

686 Phenology plays a central role in bio-geochemical cycles in conifers stands. In this study we
687 optimized different phenological models against budburst observations of six conifers species. We
688 show that all models managed to reproduce needle emergence at the site scale with good accuracy
689 (± 5 d). At the national scale, most models reproduce budburst dates with a precision of 12 days.
690 However, we highlight the need to consider both spatial and temporal variability when calibrating
691 phenological models.

692 Different budburst models performed equally independently of their complexity and the process

693 they include (forcing, chilling, photoperiod) and models calibrated at a fine spatial resolution were
694 not able to predict budburst dates when applied at coarse resolutions typical of the grid of global
695 models. This suggests that common models developed for site scale experiments might be
696 inadequate for large scale simulations. This first attempt in implementing an explicit phenological
697 model for evergreen conifer PFTs for large scale simulations managed to reproduce the observed
698 LAI dynamics both at the site and regional scale. A sensitivity analysis highlighted that the new
699 phenology module has a significant impact on the simulated carbon fluxes. We showed that needle
700 onset will be ± 11 days earlier in 2060-2100 compared to 1970-2000 and more analysis are needed
701 to quantify the effect of evergreen conifers phenology on the projected carbon budget. The findings
702 will help future research to better improve current and future predictions of carbon, water, nutrient
703 and heat cycles using ecosystem model.

704

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713

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928 **Supporting information captions**

929 Appendix SA: Litter sampling methodology, initial conditions and forcing data used for
930 ORCHIDEE simulations, sensitivity analysis

931 Appendix SB: Description, equations and parameters for the eight budburst models

932 Appendix SC: Supplementary figures and tables

