



# **Representing explicit budburst and senescence processes for evergreen conifers in global models**

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HAL Authorization

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

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

**Authors :** Marc Peaucelle<sup>1</sup>, Philippe Ciais<sup>1</sup>, Fabienne Maignan<sup>1</sup>, Manuel Nicolas<sup>2</sup>, Sébastien Cecchini<sup>2</sup>, Nicolas Viovy<sup>1</sup>

<sup>1</sup> Laboratoire des Sciences du Climat et de l'Environnement, CEA CNRS UVSQ, Gif-sur-Yvette, France

<sup>2</sup> Office National des Forêts, Département Recherche Développement et Innovation, Fontainebleau, France

Marc Peaucelle: [marc.peaucelle@lsce.ipsl.fr](mailto:marc.peaucelle@lsce.ipsl.fr) (corresponding author, phone:+33 169 088 739 /fax:+33 169 087 716 )

Philippe Ciais: [philippe.ciais@lsce.ipsl.fr](mailto:philippe.ciais@lsce.ipsl.fr)

Fabienne Maignan : [fabienne.maignan@lsce.ipsl.fr](mailto:fabienne.maignan@lsce.ipsl.fr)

Manuel Nicolas : [manuel.nicolas@onf.fr](mailto:manuel.nicolas@onf.fr)

Sébastien Cecchini : [sebastien.cecchini@onf.fr](mailto:sebastien.cecchini@onf.fr)

Nicolas Viovy: [nicolas.viovy@lsce.ipsl.fr](mailto:nicolas.viovy@lsce.ipsl.fr)

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

**Type of paper:** Primary research article

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 ( $\pm 5$  days) and at regional scale  
41 ( $\pm 12$  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  $10.3 \pm 2.8$  and  $12.3 \pm 4.1$  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 CO<sub>2</sub> 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.

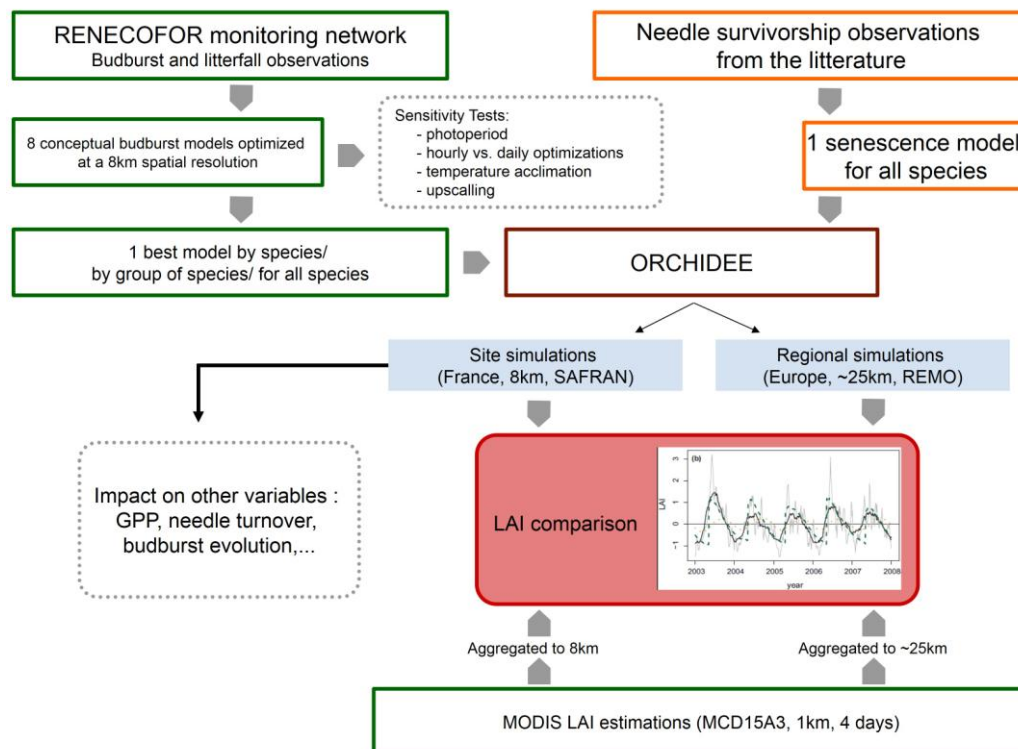
122

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

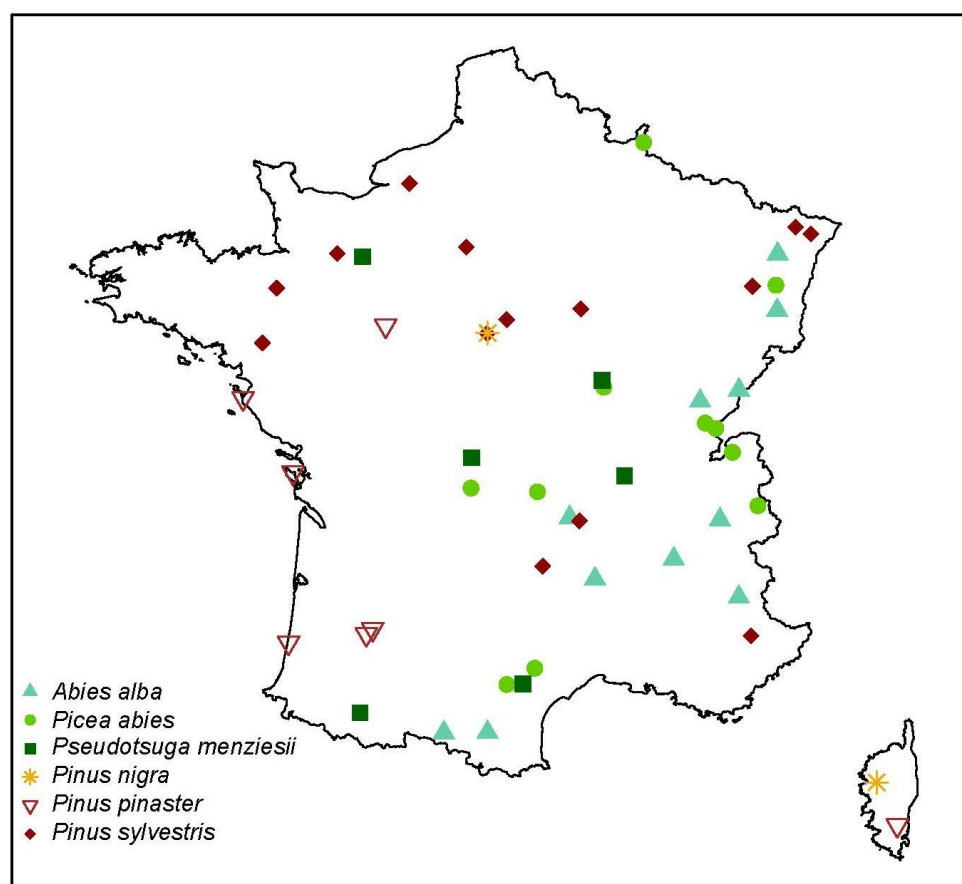
129  
130 We used budburst observations and litterfall samples collected from 1997 to 2011 over the 51 forest  
131 plots of the French RENECOFOR (REseau National de suivi à long terme des ECOsystèmes  
132 FORestiers) network covering the six main coniferous species in France (number of plots in  
133 parentheses): *Pseudotsuga mensieziei* (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  
145 **Fig. 1:** Flow chart of the model calibration and evaluation

## 2.1. Data from the RENECOFOR forest monitoring network

Visual observations of the timing of budburst were collected in 51 plots located in public forests and stratified according to the major commercial tree species grown in France. Those plots are part of the French national long-term forest monitoring network (RENECOFOR, part of the ICP – 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).



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

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

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

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

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

### 2.3. Budburst model selection criterion

The purpose of this study being to calibrate a budburst model for regional simulations, we needed a specific performance metric that characterizes the ability of this model to capture both spatial and temporal budburst gradients. Most studies have used root mean square error (RMSE, Eqn 2) or linear regression between simulated and observed budburst dates to select the best phenological model (Vitasse *et al.*, 2011; Olsson *et al.*, 2013). We argue that two performance criteria are desirable: a representation of both spatial and temporal extremes of budburst across a region, and a representation with minimal systematic spatial or temporal bias. A single metric is insufficient to account for these two criteria. To select the best set of parameters for each model, we thus propose a combined metric accounting for three key aspects of the model: the ability to reproduce extreme values, the average bias to observations and the effect of outliers. This new criterion is the Euclidean distance to optima (DIST, Eqn 3) of six weighted different metrics across sites and years. This new metrics maximizes model performances by catching both spatial and temporal variabilities of budburst and by reducing the chance to converge to local minimum during calibration. This combined metric has two components of the RMSE to limit outliers, the squared bias (BS, Eqn 4) and the squared difference between standard deviation (SDSD, Eqn 5; Kobayashi & Salam, 2000) normalized by the mean natural difference observed between sites  $SDSD_{nat}$  and  $BS_{nat}$ ; the Spearman rank correlation coefficient ( $R_s$ ), the linear regression slope ( $lm_s$ ; Eqn 6) and its associated coefficient of determination ( $lm_{R^2}$ ) between observed and modeled budburst, which captures extreme values; finally the average bias (AB, Eqn 7), and temporal and spatial biases between modeled and observed budburst dates. For the purpose of large scale simulations, more weight was given to capture bias and extremes than outliers (Eqn 3), with the sum of weighting factors equaling 1. With this metrics, the best performance is achieved when  $DIST=0$ . The different components of 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  $0.5^\circ$  ( $\sim 55$  km) maximum distance, with a  
 234 mean annual temperature difference less than  $0.5^\circ\text{C}$ , 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  $7.6 \pm 3.5$  days,  $SDSD_{nat}$  to  
 240  $3.16 \pm 5.09$  days<sup>2</sup> and  $BS_{nat}$  to  $41.76 \pm 38.46$  days<sup>2</sup>.

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 ( $\Delta AIC$ ) between  
258 AICc and the minimal AICc obtained among all models. Thus, the higher is  $\Delta AIC$ , the less  
259 parsimonious is a model. Models with  $\Delta AIC$  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 mensieziei*, 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 ( $t_o$ ; 1<sup>st</sup> of January) and chilling ( $t_c$ ; 1st of November) in order to assess the models’ robustness with

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

## 2.5. Meteorological dataset

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

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

where  $T_{obs}$  (°C) is the mean observed temperature of the site,  $T_{saf}$  (°C) the mean temperature of the site from SAFRAN dataset,  $A_{saf}$  (km) the mean altitude of the SAFRAN cell and  $A_{obs}$  (km) the altitude of the site.

## 2.6. Senescence model

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

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

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

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

Where  $S(t)$  is the survivorship probability of a needle,  $t$  the needle age (days), and  $\mu$  (days<sup>-1</sup>) and  $\lambda$  (days) parameters to be fitted on literature observations.

## 2.7. Modification of the ORCHIDEE model

The inclusion of an explicit phenology for evergreen conifers in ORCHIDEE (Krinner *et al.* 2005) needed the modification of the original model. The needle maximum age parameter for evergreen conifers, fixed at 910 days (average lifespan of *Pinus* needles) in the standard version of ORCHIDEE was modified to depend on species. This maximum age can vary considerably, going from 2 years in pine species to more than 10 years for *Abies alba* and *Picea abies* (Peaucelle *et al.*, 2016). In ORCHIDEE, the  $V_{cmax}$  parameter (maximal rate of the RUBISCO carboxylation activity in  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) increases with needle age, reaching a maximum value when the relative age of the 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  $0.07^\circ$  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<sup>-1</sup> yr<sup>-1</sup> (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

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

Species	Leaves kg ha <sup>-1</sup> yr <sup>-1</sup>	CV <sub>L</sub> %	Prop. %	Total kg ha <sup>-1</sup> yr <sup>-1</sup>	CV <sub>T</sub> %	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

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

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

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

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

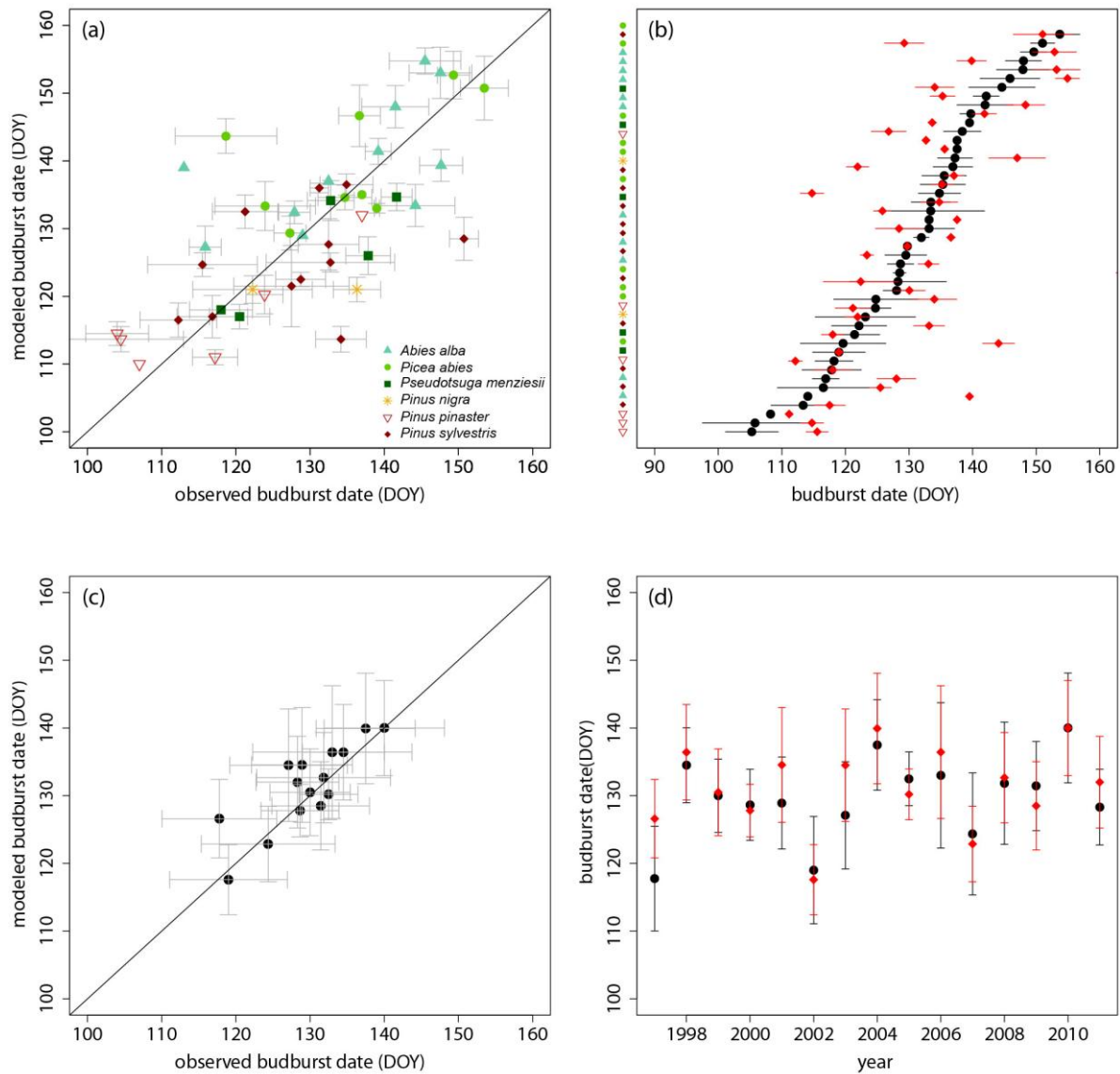
**Table 4:** Best models retained for each species according to both the predictive power considering spatial and temporal variability (DIST-ST) and the parsimony (with the lowest number of parameters). Models were optimized against daily temperatures. See Appendix SB for a detailed description of each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

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).

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 concords 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

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

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

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

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

We checked for model robustness at lower spatial resolutions, representative of typical forcing data for global vegetation models. At  $0.25^\circ$  resolution, most of DIST-ST values were higher than at a resolution of  $0.07^\circ$  and the best models differed. For all species, the best DIST-ST increased from 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 value of 0.49. Some models were no longer able to work correctly and DIST-ST values diverged

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

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

#### 3.4. Senescence model parameters

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

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

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

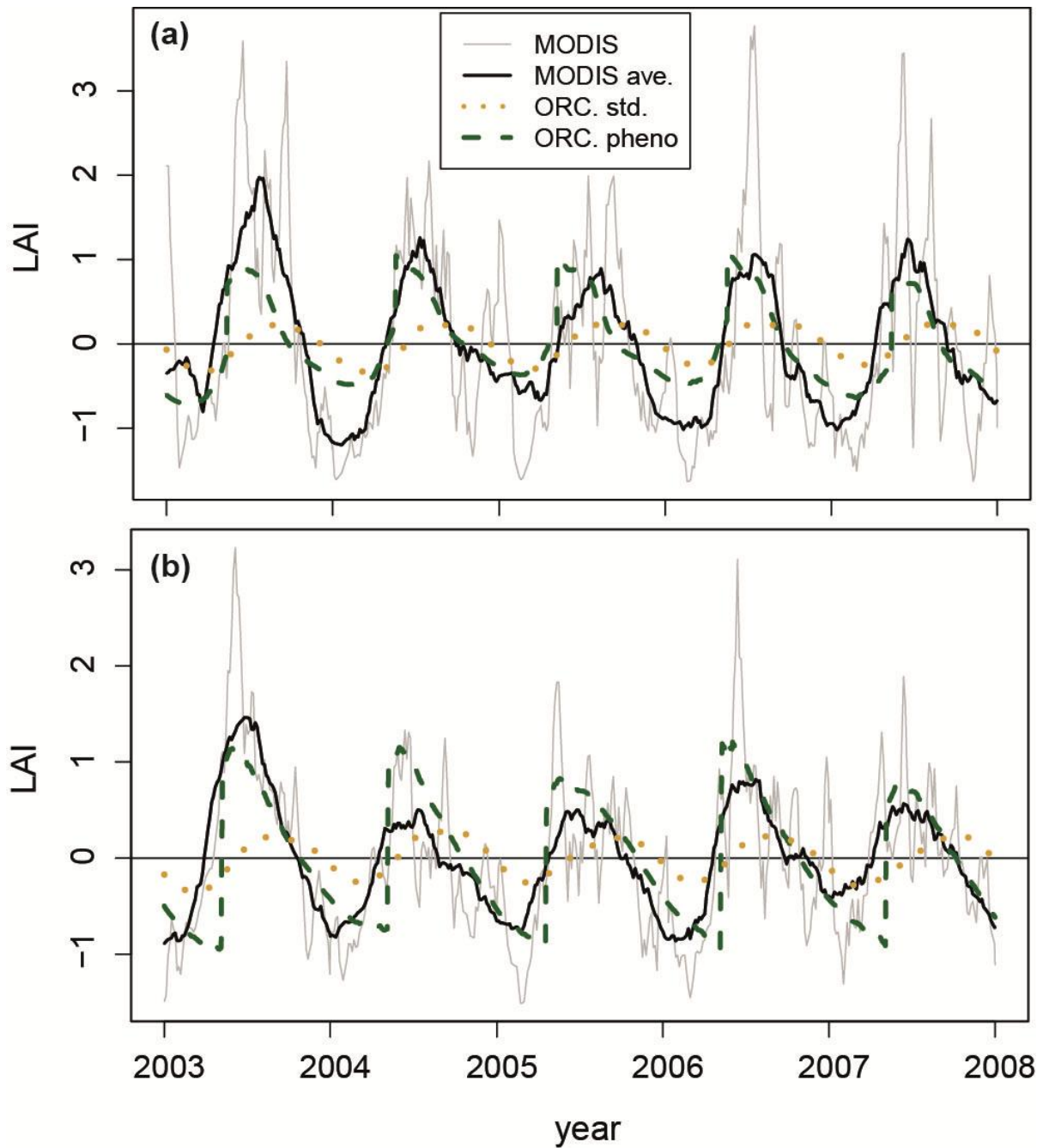
with  $Needle_{age}$  the maximal needle age.

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

### 3.5. Comparison against satellite data

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



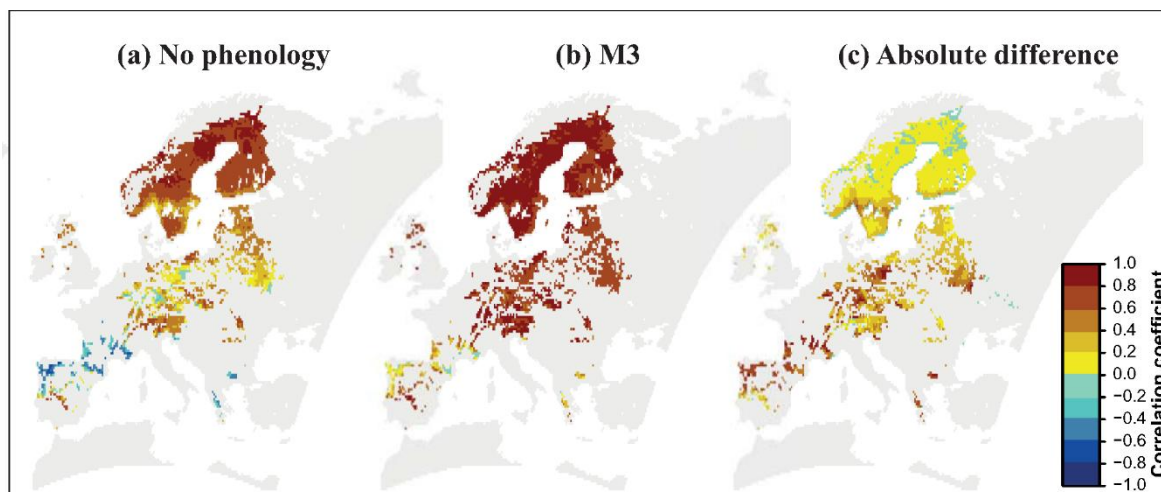


**Fig. 4:** Comparison between observed (MODIS) and simulated (model M7) LAI dynamics with ORCHIDEE for a) a *Picea abies* stand (lat=50.16°, long=5.46°) and b) a *Pinus sylvestris* stand (lat=49.25°, long=8.06°). All data are centered on the average observed (or simulated) LAI value (2003-2008). Gray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

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



516  $R=0.48\pm0.3$  to  $0.72\pm0.2$ ) 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 ( $R=0.69\pm0.2$ ). 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.

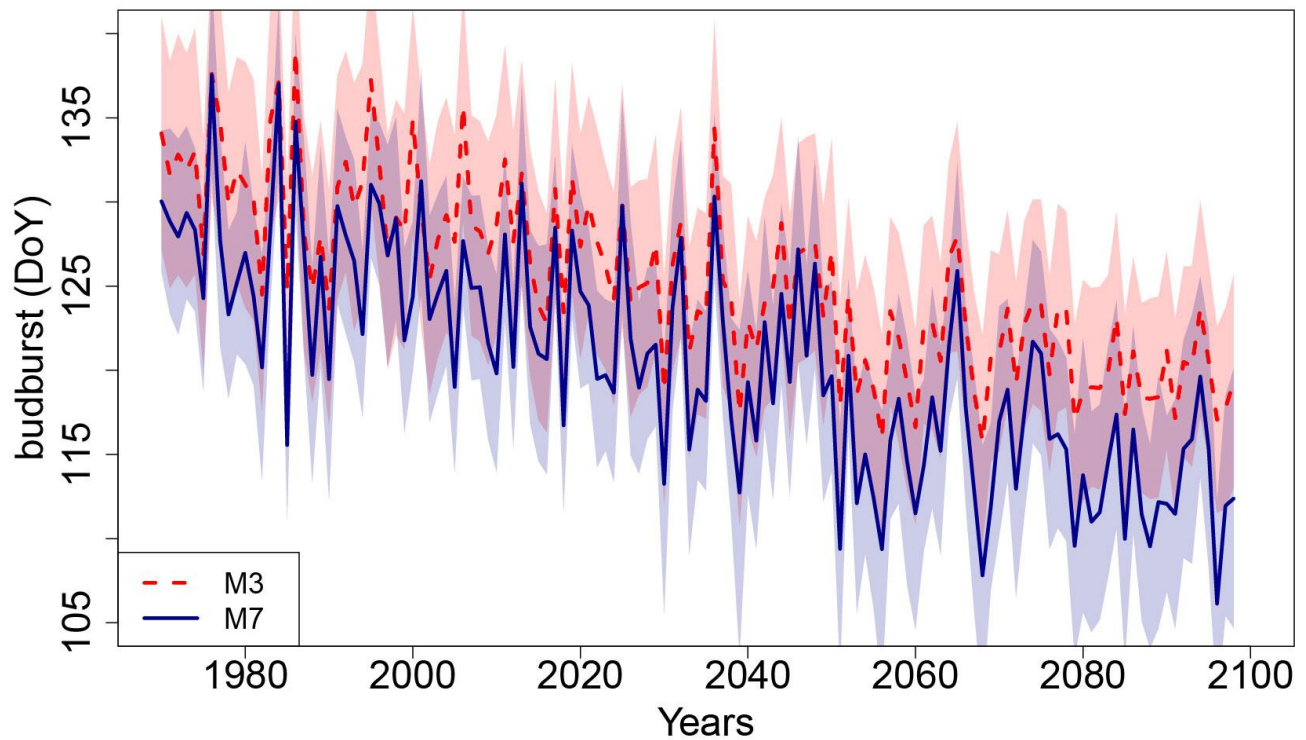


522 **Fig. 5:** Spatial representation of the correlation coefficient between MODIS estimated LAI and  
 523 ORCHIDEE simulated LAI at a  $0.25^\circ$  spatial resolution averaged over the period 2000-2007: a) in  
 524 the standard configuration without explicit phenological processes, or b) with the 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 mensiezi*). The correlation is calculated for pixels with a minimal coniferous fraction  
 528 cover of 20%.  
 529  
 530  
 531  
 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= $-0.126\pm0.01$  days  $\text{yr}^{-1}$ ,  $R^2$   
 538  $=0.57\pm0.06$ ). Compared to 1970-2000, projections indicated an advancement of the budburst date of  
 539 coniferous species of  $10.3\pm2.8$  and  $12.3\pm4.1$  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 ( $4.8\pm0.8$  days) over

542 the period 1970-2100.



543 **Fig. 6 :** Temporal evolution of the mean budburst dates (DOY) simulated over France from 1970 to  
544 2100 for models M3 and M7 (all species together). For each line, the corresponding colored area  
545 indicates one s.d. either side of the mean.  
546  
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 ( $845.3 \pm 55.5$  days for spruces versus  $1740 \pm 18.8$  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

reach their maximal activity only 3 months after unfolding, simulated GPP was not sensitive to changes in budburst date. By imposing the needle onset (from day 90 to 160), we observed a mean 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 for each day difference in budburst.

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

## 4. Discussion

### 4.1. Uncertainties in model validation

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

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

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

The senescence model proposed in this study defines a continuous process over the needle lifespan. Moreover, we fixed the length of the period of needle accretion in ORCHIDEE, which can result in biases in LAI at the beginning of the growing season. We argue that an optimization of the 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,



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

## 5. Conclusion

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

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  $\pm 11$  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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927

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

