



**HAL**  
open science

# Process-Based Models of Phenology for Plants and Animals

Isabelle Chuine, Jacques Régnière

► **To cite this version:**

Isabelle Chuine, Jacques Régnière. Process-Based Models of Phenology for Plants and Animals. Annual Review of Ecology, Evolution, and Systematics, 2017, 48 (1), pp.159-182. <10.1146/annurev-ecolsys-110316-022706>. <hal-03780498>

**HAL Id: hal-03780498**

**<https://hal.science/hal-03780498v1>**

Submitted on 19 Sep 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire HAL, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



HAL Authorization

3  
4 **Title**

5 Process-Based Models of Phenology for plants and animals

6  
7 **Authors**

8 Isabelle Chuine<sup>1§</sup> and Jacques Régnière<sup>2</sup>,

9  
10 1 CEFE-CNRS, Montpellier, France, [isabelle.chuine@cefe.cnrs.fr](mailto:isabelle.chuine@cefe.cnrs.fr)

11 2 Natural Resources Canada, Canadian Forest Service, Québec, Canada,  
12 [jacques.regniere@canada.ca](mailto:jacques.regniere@canada.ca)

13  
14 § Corresponding author

15 Isabelle Chuine, Centre d'Ecologie Fonctionnelle et Evolutive, UMR CNRS 5175, 1919 route  
16 de Mende, F-34093 Montpellier, cedex 05, France. [isabelle.chuine@cefe.cnrs.fr](mailto:isabelle.chuine@cefe.cnrs.fr)

17  
18 **Keywords**

19 Annual cycle, extratropical species, diapause, dormancy, environmental control, response  
20 functions, parameter estimation

21 **1 Summary Points**

- 22 1. Phenology models for plants and ectotherms share several characteristics in their  
23 structure and mathematical functions representing responses of organisms to  
24 environmental factors because of the many similarities in the environmental control of  
25 their developmental cycles.
- 26 2. Divergences in phenology modelling for plants and animals are mostly due to  
27 specificities of the questions addressed. Many animal models tackle issues at the  
28 population level and take explicit account of individual variability, whereas plant models  
29 focus on physiological issues and are often concerned with the average plant at the  
30 species or variety level.
- 31 3. Phenology models for plants and ectotherms share the same shortcomings: they do not  
32 take into account the geographical variability in model parameters due to local adaptation  
33 to climate; they do not take into account the potential acclimation of developmental  
34 responses to temporally variable environmental factors; they are defective in modelling  
35 accurately the resting stage and the effects of photoperiod.
- 36 4. Process-based phenology model parameters are difficult to estimate and accurate  
37 estimation requires a combination of statistical and experimental inference.
- 38 5. Plant and animal phenology modelling have not cross-fertilized so far. Respective  
39 research communities could learn from each other to advance our understanding of the  
40 mechanisms of developmental timing.

41 **Abstract**

42 Phenology is a key aspect of plant and animal life strategies that determines the ability to  
43 capture seasonally variable resources. It defines the season and duration of growth and  
44 reproduction, and paces ecological interactions and ecosystem functions. Phenology models  
45 have become a key component of models in agronomy, forestry, ecology, and biogeosciences.  
46 Plant and animal process-based phenology models have taken different paths that have so far  
47 not crossed. Yet, they share many features because plant and animal annual cycles also share  
48 many characteristics, from their step-wise progression including a resting period, to their  
49 dependence on similar environmental factors. We review the strengths and shortcomings of  
50 these models and the divergences in modelling approaches for plants and animals, which are  
51 mostly due to specificities of the questions they tackle. Finally we discuss the most promising  
52 avenues and the challenges phenology modelling needs to address in the upcoming years.

53

## 54 **2 Introduction**

### 55 **2.1 Why are phenology models important?**

56 Appropriate seasonal timing is a basic ecological requisite for all organisms as their life-  
57 cycle must be keyed to the appropriate seasonal cycles of climate or resources. The phenology  
58 of plants is a key regulator of ecosystem processes and biosphere feedbacks to the climate  
59 system (Richardson et al. 2013). It regulates ecosystem productivity (Richardson et al. 2012),  
60 and more broadly ecosystem carbon cycling (Delpierre et al. 2009b), water (Hogg et al. 2000),  
61 nutrient cycling processes (Cooke & Weih 2005) and energy balance (Wilson & Baldocchi  
62 2000). At the community level, food webs largely depend on developmental timing of the  
63 interacting species. For example, the fitness of insect herbivores feeding on plants often  
64 depends on the timing of appearance of young palatable leaves (Pureswaran et al. 2015) with  
65 consequences all the way up the food web (Godfray et al. 1994; Visser & Holleman 2001; Stoks  
66 et al. 2005). Phenology is also one of the most important phenotypes considered in varietal  
67 selection in agronomy as it determines the yield and the organoleptic quality of the harvest  
68 (Nissanka et al. 2015; Alderman & Stanfill 2017).

69 Growing evidence of the key importance of seasonal timing for growth, performance, and  
70 fitness has inspired research in agronomy, ecology and environmental sciences to elucidate and  
71 model environmental controls on phenology and predict how it will respond to ongoing climate  
72 change. The timing of developmental stages is indeed largely dependent on environmental cues.  
73 Phenology models have thus become a key component in models of crops (Nissanka et al.  
74 2015), Earth systems (Dahlin et al. 2015), population dynamics (Anderson et al. 2013; Maino  
75 et al. 2016), species distribution (Chuine 2010; Régnière et al. 2012a), and evolutionary  
76 dynamics (Asbury & Angilletta 2010; Donohue et al. 2015; Duputié et al. 2015). A detailed  
77 description of why phenology models are an important component of these different models is  
78 presented in Supplemental Materials Section S1.

79

## 80 **2.2 Comparison of plant and animal seasonal biology**

81           Plants and insects share several features of their developmental cycle. Figure 1 provides  
82 a comparative overview of the most common annual cycles of insects and plants, which  
83 especially highlights the convergence between insects and perennial plant cycles where, for  
84 example, diapause is equivalent to endodormancy, and quiescence to ecodormancy (Considine  
85 & Considine 2016). In most animals, reproduction occurs in the last (adult) life stage, separated  
86 in time from growth and other functions. In annual or biennial plants, reproduction also takes  
87 place when growth stops and leads to death, while the two functions can take place  
88 simultaneously in perennials, especially woody plants. For example, in many temperate and  
89 boreal tree species, flowering and fruiting take place at the same period as leaf unfolding and  
90 growth, and secondary growth respectively. Species with obligate diapause or estivation usually  
91 exhibit discrete (distinct, non-overlapping) generations, as a result of the strong life-cycle  
92 synchronization imposed by the resting period occurring in a specific life stage. However, in  
93 the absence of such strong synchronization, multiple generations can coexist, posing particular  
94 ecological problems such as inter-generational competition or mate finding (Yamanaka et al.  
95 2012).

96           Most ectotherms and extratropical plant species have the ability to enter a resting stage  
97 during seasons unfavorable to growth, resource acquisition or reproduction. This period is a  
98 key adaptation to seasonal climates. It is called diapause in animals (Hand et al. 2016) and  
99 endodormancy for buds or dormancy for seed in plants (Lang et al. 1987). It takes place in  
100 winter in temperate climates and for most species in Mediterranean climates, and in summer in  
101 arid subtropical climates. In many cases, animal and plant species have evolved an inflexible  
102 “synchronizing” mechanism through obligatory rest. Diapause controls voltinism in many  
103 insects. Species that do not have a clear diapause exhibit complex life cycles (Powell & Logan

104 2005). But many animal species display optional diapause or estivation in one or more life  
105 stages as a more flexible life-history strategy to avoiding unfavorable periods such as dry season  
106 or winter. In most organisms, this rest period is broken by the cumulative action over time of  
107 cold temperatures, dry weather, drought-breaking rainfall (Speybroek et al. 2006) or simply  
108 time passed (Delisle et al. 2009). Similarly, many plant species display cyclical dormancy of  
109 buds or seeds, controlled by seasonal environmental cues. However, in contrast with insects,  
110 which show sequential and unique resting life stages at the whole-organism level, plants are  
111 modular organisms showing some degree of independence of their different organs (leaf, wood,  
112 root, flower, fruit) that can each have their own developmental cycle (Delpierre et al. 2016).

113

### 114 **2.3 Comparative overview of environmental cues in plant and animal phenology**

115 Another common feature of plant and insect phenology is the environmental control of  
116 their developmental rates. In both types of organisms, temperature, photoperiod, water and  
117 nutrient availability, in order of importance, either alone or in interaction with each other, are  
118 used as cues at different stages of development (Photoperiod: Hand et al. 2016; Zohner et al.  
119 2016; temperature and photoperiod: Fantinou et al. 2004; Caffarra et al. 2011a; food: Murillo-  
120 Rincón et al. 2017; photoperiod and food: Ridsdill-Smith et al. 2005; moisture: Stoks et al.  
121 2005; Misson et al. 2011; temperature and humidity: Jaworski & Hilszczanski 2013).

122 Temperature is the strongest determinant of plant and insect phenology whatever the  
123 species. Warmer temperatures accelerate the rate of cell elongation in plants, as well as  
124 metabolic, developmental and reproductive rates in insects. Cooler temperatures have a dual  
125 effect in plants depending on the cycle's period, which can generate errors of interpretation in  
126 experiments. On one hand, cool temperatures activate the stress response pathway in plants and  
127 thereby the induction of endodormancy, and leaf senescence (Cooke et al. 2012). On the other  
128 hand, accumulation of cool temperatures during endodormancy or vernalisation respectively

129 releases dormancy or promotes flowering (Cooke et al. 2012). A period at cool temperature, or  
130 simply the passage of time, is also required to end diapause in animals.

131         Photoperiod plays a less universal role. It does not affect all developmental transitions,  
132 and species differ in their sensitivity to this cue. Zohner et al. (2016) found that about one third  
133 of extratropical tree species were sensitive to photoperiod but the magnitude of the effect on  
134 leaf out phenology was generally minor in 95% of species. In plants, photoperiod plays a role  
135 in growth cessation, bud set, dormancy induction, and leaf senescence (chlorophyll net  
136 production). In many animals, it is the diapause trigger. In both plants and animals, photoperiod  
137 can also interact with temperature and alter the development rate or cell elongation rate. In  
138 environments where day length varies little, such as the tropics, animals use a variety of other  
139 diapause-induction cues such as temperature, precipitation, food quality, even population  
140 density (Hand et al. 2016).

141         In both animals and plants, nutrition and water availability have less important effects  
142 on phenology, except under extreme conditions (Misson et al. 2011; Jaworski & Hilszczanski  
143 2013). However, nutrition seems more important in the growth and development of animals, as  
144 it can slow or accelerate development rates, and even induce summer diapause (Ridsdill-Smith  
145 et al. 2005; Stoks et al. 2005; Murillo-Rincón et al. 2017), while water availability seems more  
146 important in the growth of plants as cell elongation necessitates a minimal turgor pressure and  
147 water availability also affects nutrients uptake. Finally, both in plants and animals, living  
148 circumstances can alter the developmental pathways in fundamental ways. In frogs,  
149 intraspecific competition (so-called priority effects) can alter compensatory developmental  
150 acceleration responses to delayed hatch, and may help explain the maintenance of synchronous  
151 life histories (such as explosive breeding) in seasonal environments (Murillo-Rincón et al.  
152 2017). Compensatory developmental and growth responses have been found in a damselfly,

153 associated with photoperiod, food resources and predation pressure (Stoks et al. 2005). In  
154 plants, herbivory is also known to affect phenology (Palacio et al. 2013).

155 This short comparative overview shows that insect phenology is more temperature-  
156 driven, and less photoperiod- or water-driven than it is in plants. It may also be somewhat less  
157 dependent on cool winter temperatures. As a result, global warming may affect their respective  
158 phenology differently. However, because herbivore fitness is very much dependent on  
159 synchrony with their host plants, and because many have short generation times, we might also  
160 expect that life cycle asynchrony induced by global warming could lead to rapid herbivore  
161 adaptation through natural selection.

162

## 163 **2.4 Scope of the review**

164 In this review we focus on process-based phenology models (not on analytical or statistical  
165 phenology models) that describe known or hypothetical cause-effect relationships between  
166 physiological processes and some driving factors in the organism's environment to predict the  
167 precise occurrence in time of various phenological events. We provide an overview of process-  
168 based phenology models used for plants and animals, focusing on their similarities and  
169 differences. We discuss their shortcomings and the main challenges for future research. We  
170 have restricted our review to extra-tropical regions for space reasons. Examples used in this  
171 review are biased towards insects for animals and trees for plants, but most of the rationale,  
172 methods and models we describe are applicable to all plants and ectotherms.

173

## 174 **3 History of phenology models**

### 175 **3.1 From degree days to non-linear models**

176 Phenology modelling has a long history starting in 1735 with a publication by de Reaumur  
177 (1735) introducing the concept of degree-day sum. He proposed that plant development is

178 proportional to the sum of temperature over time rather than to temperature during the  
179 phenological event itself. This is still the most important assumption in plant and animal  
180 phenology modelling. Interest in phenology modelling was rekindled in the late 20<sup>th</sup> century  
181 because of the revolution in computer science, the advent of integrated pest management and  
182 growing concern about global climate change. Since 1980 the number of articles dealing with  
183 phenology modelling has increased almost exponentially (from 50 in 1991 to over 500 in 2016),  
184 and most of them have been dedicated to proposing and validating new models, or comparing  
185 models.

186         The overwhelming influence of temperature on the performance of plants and ectotherms  
187 has led to the development of the Metabolic Theory of Ecology (MTE; Brown et al. 2004;  
188 Schramski et al. 2015), that we detail in Supplemental Materials Section S2. Central to the MTE  
189 is its description of the Universal Temperature Dependence (UTD) of ecological processes,  
190 from metabolism to ecological interactions, based on the Boltzmann factor, a simple  
191 exponential function of temperature borrowed from the theory of statistical mechanics of gases  
192 (equation [S1] Supplemental Materials Section S2). Many authors have suggested that the UTD  
193 could be made more realistic if the Boltzmann factor was replaced by a unimodal response  
194 function covering the entire range of temperatures that organisms are exposed to in nature  
195 (Knies & Kingsolver 2010). An appropriate UTD function must display characteristic optimum  
196 ( $T_{opt}$ ) and critical minimum ( $CT_{min}$ ) and maximum ( $CT_{max}$ ) temperatures (Pörtner et al. 2006;  
197 Deutsch et al. 2008; Kingsolver 2009; Asbury & Angilletta 2010). The critical temperatures  
198 result from the inactivation (reversible denaturation) of enzymes at extreme temperatures, and  
199 reduce the efficiency of metabolic reactions (equation [S3]; Fig. S1).

200

### 201 **3.2 From event prediction to individual-based models**

202 Modelling plant and animal phenology took two separate pathways that have not crossed  
203 so far. Yet, they share several common features. In both cases, models started to be developed  
204 in the 1950s, and at first focused on specific phenological stages: leafing and flowering in plants  
205 (Weinberger 1950) and primarily in cultivated plants until the 1980s (Chuine et al. 2013); or  
206 appearance of target life stages for monitoring or control under the integrated pest management  
207 paradigm in animals, mostly insects (Kogan 1998). While plant phenology models covering the  
208 whole annual cycle have been developed for crops (e.g. Nissanka et al. 2015; Alderman &  
209 Stanfill 2017), such models for wild plants are still rare (but see e.g. Burghardt et al. 2015 for  
210 Arabidopsis; Chuine & Beaubien 2001 for tree species). This is because autumn phenophases  
211 such as leaf senescence and fruit maturation have received much less attention than spring  
212 phenophases so that observations and experimental results available to define, calibrate and  
213 validate models are still scarce, and either concern forest trees for leaf senescence (Delpierre et  
214 al. 2016) or crops for fruit maturation (e.g., Soltani et al. 2006; but see Mutke et al. 2003).  
215 Moreover, very few studies so far have attempted to model the phenology of wood (Takahashi  
216 & Koike 2014), and no model incorporates the phenology of fine roots and more broadly the  
217 phenology of nutrient, water, carbon and energy fluxes in a single scheme.

218 Models of insect phenology are increasingly concerned with the succession of life stages  
219 throughout their entire life cycle from egg to adult, including reproduction and survival, in  
220 response to climate (Logan et al. 2003; Régnière et al. 2012a; Sporleder et al. 2013). This  
221 holistic view of life-cycle modelling has triggered increasing attention on the realistic  
222 incorporation of individual and microclimatic variability and methods to describe and simulate  
223 them in models. Early attempts at doing this used a variety of techniques such continuation  
224 ratios using degree-day accumulation (Candy 1991). The majority of insect phenology models

225 rely on a “cohort” approach, where accounting of development is done for distinct cohorts based  
226 on the variability of development times (Logan 1988).

227         Increasingly however, individual-based models are being developed to accommodate  
228 the complexity of animal life histories (DeAngelis & Grimm 2014). They facilitate the  
229 introduction of developmental pathway bifurcations such as facultative entry into diapause, the  
230 co-existence of multiple, single and partial generations per year, and the variation of  
231 developmental responses between individuals (de Jong & van de Have 2009; Régnière et al.  
232 2015). Simulation of individual variation is discussed in more detail in Supplemental Materials  
233 Section S2. While individual-based models have the burden of high memory and computing  
234 power, they offer many advantages in terms of mathematical simplicity and flexibility  
235 (Régnière et al. 2015). They also constitute a ready platform for modelling natural selection  
236 processes in animals (Moustakas & Evans 2013; Redaubo et al. 2013) as well as in plants  
237 (Warren & Topping 2001).

238

## 239 **4 A comparative overview of plants and animals process-based phenology models**

240         Several recent papers compare phenology models, for either plants (Hänninen & Kramer  
241 2007; Chuine et al. 2013; Olsson et al. 2013; Basler 2016) or animals (Niehaus et al. 2012;  
242 Colinet et al. 2015). Here we present a comparative overview of both plant and animal  
243 phenology models, but do not present an exhaustive list of models that can be found in these  
244 papers. We made here the choice of highlighting similarities and differences between plant and  
245 animal phenology models.

246

### 247 **4.1 Philosophy and structure of the models**

248         Process-based phenology models formally describe known or hypothetical cause-effect  
249 relationships between physiological processes involved in the developmental cycle of

250 organisms and some driving factors in the plant's environment. The structure of process-based  
251 models is usually based on systems theory rather than statistical inference (Hänninen & Kramer  
252 2007). New relationships are allowed in such models only if information on their impacts on  
253 the modeled processes is available. It is important to note that parameters of mechanistic models  
254 have physical dimensions that can, in principle, be measured directly instead of being  
255 statistically inferred. However, this is not always possible, especially for some particular phases  
256 such as endodormancy induction and termination in plants because this state of development is  
257 particularly difficult to assess. This is why so little modelling of diapause itself has been  
258 attempted in ectotherms (Hodek 1996). Process-based phenology model structure and  
259 hypotheses are thus built on experimental results on the environmental control of particular  
260 development phases obtained under controlled conditions.

261 Process-based plant phenology models have taken a new turn due to the recent availability  
262 of high-throughput phenotyping techniques (Nagano et al. 2012; Satake et al. 2013; Kudoh  
263 2016). Recent advances in molecular biology, cell biology and metabolomics have shed a new  
264 light on the molecular basis of temperature and photoperiod responses of cell activity in model  
265 organisms such as *Arabidopsis* and Poplar (Bratzel & Turck 2015; Singh et al. 2016). Similar  
266 progress is being made concerning the processes of diapause in insects (Xiongbing et al. 2015;  
267 Hand et al. 2016; Kang et al. 2016). However, very few studies have incorporated this  
268 knowledge into predictive models so far.

269 Phenology models for the entire annual cycle of a plant or an animal can be seen as  
270 metamodels composed of several sub-models describing each a component of the cycle, i.e. a  
271 phenophase such as flowering in plants, or a life stage such as a larval instar in insects (Fig. 2).  
272 Development is represented by a state variable,  $S$  for development Stage, which is the  
273 summation of development over time (in steps of days, hours or minutes) from a start date  $t_0$ ,  
274 as a function of environmental cues. If the cycle comprises  $n+1$  development phases (Fig. 2),

275 by definition  $S_0 = 0$  in the initial stage (e.g. seed germination, egg hatch), and  $S_n$  reaches some  
 276 maximum value ( $S_n^*$ ) at the end of the last stage (often defining an annual cycle). Each  
 277 phenophase (or life stage)  $k$  starts at  $t_k$  and ends at time  $t_{k+1}$  when  $S_k$  reaches a value  $S_k^*$ , which  
 278 is specific to the model. Each phenophase is described by a sub-model determining its reaction  
 279 norms  $f$  to various cues ( $T$ : temperature,  $P$ : photoperiod,  $W$ : water,  $L$ : light,  $N$ : nutrient,  $B$ :  
 280 stressful biotic interaction). Response functions combine by addition (+), multiplication ( $\times$ ) or  
 281 composition ( $\circ$ ). Phases are either sequential (follow each other in time) or overlap (one phase  
 282 can start before the end of the previous phase). The general structure of process-based  
 283 phenology models is thus:

$$284 \quad t_k \text{ such that } S_{k,t} = \sum_{t_{k-1}}^{t_k} R_{k,t}(Z) = S_k^* \quad [1]$$

285 Virtually any phenology model can fit into this framework. Models essentially differ in  
 286 the number of phases  $n$  they distinguish and in the functions describing each phase's  
 287 development rate  $R(Z)$  (Figs. S2, S3). For example, a single-phase Growing Degree Day model,  
 288 the simplest phenology model with only three parameters, can be written as:

$$289 \quad t_1 \text{ such that } S_t = \sum_{t_0}^{t_1} R_t(T) = S^* \text{ where } R_t(T) = \begin{cases} T_t - T_b & \text{if } T_t > T_b \\ 0 & \text{otherwise} \end{cases} \quad [2]$$

290 where  $T_t$  is daily mean temperature,  $t_0$  is the starting date of the phenophase,  $T_b$  is the threshold  
 291 temperature and  $S^*$  is the degree-day sum required to complete the phenophase (at  $t_1$ ).

292 In annual plants and univoltine animals, phenophases are sequential so that sub-models  
 293 do not interact with each other except for their start date that corresponds to the end date of the  
 294 previous phase. Many insect models have the distinction of representing the development of a  
 295 population of individuals (or cohorts of individuals), whereas most plant models (see  
 296 hydrothermal models for seedbanks) represent the development of the average individual of a  
 297 population/variety. In many models, an individual advances by one life stage when  $S$  reaches

298 an integer value (e.g., hatch, molt, metamorphosis), each individual having its own specific  
299 development rate. The developmental progression of a population is a compilation of a large  
300 number of individuals. In cohort-based models, it is the value of  $S_k^*$  at which a cohort changes  
301 life stage that is subject to a distribution. Plant models usually do not simulate the phenology  
302 of a population of plants (except for seed), but they simulate the phenology of the different  
303 organs of the plant, using one phenology model for each event such as bud dormancy, leaf  
304 unfolding, flowering, fruit growth and maturation, leaf senescence (e.g. Chuine & Beaubien  
305 2001; Nissanka et al. 2015; Alderman & Stanfill 2017). The variability of developmental timing  
306 among similar organs (e.g. leaves, flowers) within a plant is a level of complexity that has never  
307 been incorporated into the models so far, but would probably increase their accuracy especially  
308 in the case of tree models.

309         Some animals, such as mites and most adelgids, can have very complex life cycles with  
310 different morphs in the adult stage. In tree species, model structure can be more complex  
311 because of the specific phenology of the different organs that can overlap. Moreover, some  
312 phenophases such as leaf unfolding or flowering can even be decomposed into several sub-  
313 phases such as endodormancy (inability of cells to elongate despite favorable environmental  
314 conditions) and ecodormancy (ability of cells to elongate if environmental conditions are  
315 favorable to growth) that might also overlap. Some studies indeed suggest that endodormancy  
316 is a dynamic process and that ecodormancy can start before endodormancy has been fully  
317 released (Cooke et al. 2012). In view of this, an important concept for tree phenology models  
318 is the growth competency function introduced by Hänninen (1990), which represents the level  
319 of endodormancy and regulates the ability to grow when environmental conditions are favorable  
320 (Olsson et al. 2013). Similar cases can be found in the diapause of many insects, a fact that  
321 prompted Hodek (1996) to use the phrase “diapause is never over” to illustrate that the

322 completion of diapause and return to normal thermal response can be gradual. This is taken into  
323 account in some insect phenology models (Régnière et al. 2012a).

324 Rates of development are in most cases solely calculated as a function of temperature.  
325 However, lately, new models for trees have tried to incorporate new insights on the  
326 physiological basis of cell activity, modulating the development rate by other cues such as  
327 photoperiod (Caffarra et al. 2011b) or coming back to transition state theory by modelling the  
328 dynamics of a growth promotor/inhibitor system (Schaber & Badeck 2003).

329 Other environmental variables such as light spectral quality, water availability,  
330 nutrients; and biotic variables, such as pathogen or herbivore attacks are also known to alter  
331 the developmental cycle but have not been taken into account in models so far.

332

## 333 **4.2 Response functions to environmental cues**

334 The focus of phenology modelling efforts has been to relate temperature to phenological  
335 events, so most response functions describe the effect of temperature. In animals as in plants,  
336 many phenology models are based on the degree-day linear approximation. To account for  
337 population-level variability, many have used the continuation-ratio approach of Candy (1991)  
338 in insect models. While many authors still describe plant and insect developmental responses  
339 to temperature using linear regression (under the degree-day paradigm), the nonlinearity and  
340 unimodality of thermal responses seem ubiquitous when they are measured over the whole  
341 range of temperatures that life is exposed to in nature (see Supplementary Materials Section  
342 S3).

343 The complexity of the Schoolfield et al. (1981) equation [S3], describing an asymmetrical  
344 unimodal response to temperature, spurred an ever-increasing suite of approximations designed  
345 to achieve the same unimodal behavior with fewer, easier to guess, parameters. Many of those  
346 functions were presented together elsewhere (Régnière et al. 2012b; Chuine et al. 2013), and

347 the most widely used functions are illustrated in Figures S2 and S3. An exhaustive library of  
348 these functions for plants can also be found in the PMP freeware at:  
349 [www.cefe.cnrs.fr/fr/recherche/ef/forecast/phenology-modelling-platform](http://www.cefe.cnrs.fr/fr/recherche/ef/forecast/phenology-modelling-platform). The Gaussian  
350 distribution has been used to model development in some species (e.g. Jia et al. 2016) or to  
351 discuss issues of adaptation (Ashbury & Angilletta 2010), mainly because of its familiarity and  
352 its two intuitively simple parameters: mode (mean) and spread (variance). Other symmetrical  
353 unimodal functions have been used for plants (Chuine et al. 2013). However, symmetrical  
354 functions and functions that are non-zero over the entire range of temperature, do not describe  
355 actual thermal responses very well. Other functions, with increasing numbers of parameters,  
356 approximate the shape of equation [S3] with varying degrees of success, many making use of  
357 upper and lower critical temperatures as thresholds below and above which a biological process  
358 ceases completely (see Régnière et al. 2012b for animals; Chuine et al. 2013 for plants). The  
359 actual existence of such thresholds is questionable, because they are very difficult to measure  
360 due to excessive mortality when organisms are kept at those temperatures for long periods. In  
361 the context of degree-day calculations, they are essentially statistical features needed for  
362 calculation. In the context of non-linear development summation, their precise values are less  
363 critical, and they are used mostly as convenient cut-points for calculation. Nevertheless, the  
364 upper threshold has been discussed as a characteristic maximum critical temperature ( $CT_{max}$ ) in  
365 papers on adaptation to climate change (Deutsch et al. 2008).

366 More recently, response functions to other cues have been introduced in phenology models  
367 for plants, especially for photoperiod (Schaber & Badeck 2003; Caffarra et al. 2011b), but  
368 response functions used are similar to some already used for temperature. However, cues can  
369 sometimes interact in complex ways. For example, in the model of Caffarra et al. (2011b),  
370 photoperiod compensates for a lack of chilling temperature during endodormancy and the mid-  
371 response photoperiod of the sigmoid response function varies with the amount of chilling

372 received. Similar modifying influences of photoperiod on insect development have been  
373 modelled successfully (Ridstill-Smith et al. 2005; Jia et al. 2016).

374

### 375 **4.3 Parameter estimation**

376 The major problem faced with process-based phenology models so far was that the basic  
377 biochemistry and biophysics of certain phases was incompletely understood, and estimation of  
378 response function parameters in experimental controlled conditions is very time consuming and  
379 cannot be achieved for all species. When direct measurements of model parameters cannot be  
380 made, two estimation approaches are used: the experimental approach, that analyzes the  
381 temperature response of growth and development under controlled conditions; and the  
382 statistical approach, that uses statistical inference techniques.

383 Phenological observations used to develop, parameterize and validate phenology  
384 models have thus two main origins: historical observations in the field for cultivated species,  
385 and experimental results under controlled conditions in greenhouses, growth chambers or  
386 incubators. The accompanying meteorological data consequently often comes from different  
387 sources as well. Phenological observations in gardens or in experiments are usually  
388 accompanied by on-site meteorological observations. But phenological observations on wild  
389 populations are most often linked to off-site weather stations that can be relatively distant. In  
390 addition, many insects are exposed to microclimates that are determined by their habitat.  
391 Information on temperature in those habitats is usually lacking, and some form of microclimatic  
392 modelling is required to estimate temperature in the soil (Parton and Logan 1981), under the  
393 bark (Tran et al. 2007) or in growing shoots (Régnière et al. 2012a).

394

#### 395 4.3.1 Experimental approach

396 The experimental approach consists of experiments carried out under controlled  
397 conditions to analyze the underlying mechanisms of phenological responses, one mechanism at  
398 a time. This method has been very useful in animal phenology modelling, less so in plants,  
399 especially in trees, probably because of the logistical difficulty of conducting controlled  
400 experiments on such large organisms.

401 For insects and other small organisms, the experimental approach has been extensively  
402 used to determine the developmental, reproductive and survival responses to temperature (see  
403 Régnière et al. 2012b for statistical methods, and Seehausen et al. 2017 for a recent example),  
404 photoperiod in interaction with circadian clocks (Saunders 2014), and moisture (Jaworski &  
405 Hilszczanski 2013).

406 For plants, the experimental approach is primarily used to decipher the environmental  
407 factors affecting development. Pioneering work has been conducted by Sarvas (1972) on trees,  
408 and later on by Hänninen (1990), who tested experimentally several hypotheses concerning the  
409 environmental control of endodormancy release, and especially on its progressive nature  
410 (sequential vs overlapping phases leading to the Sequential vs Parallel models). Later on, the  
411 complex action of photoperiod on bud break was also revealed by experimental results (Caffarra  
412 et al. 2011a; Zohner et al. 2016). The experimental approach also allows estimating the  
413 parameters of the response functions to the environmental variables. One of the most easily  
414 measured responses is the temperature response of development rate during ecodormancy or  
415 quiescence, which corresponds to the response function of cell growth to temperature in plants  
416 (Sarvas 1972). We know that this function increases with temperature in a sigmoid fashion up  
417 to 25-30°C, and would probably show an optimum had higher temperatures been tested. By  
418 varying the temperature conditions experimentally over a wide range, the shape of the function  
419 can be determined precisely for different species, varieties, and genotypes. Other experiments

420 on plants are also used to measure indirectly the progress of endodormancy release using  
421 regrowth tests where seedlings are incubated at growth-promoting temperatures following a  
422 period of chilling, with both the chilling duration and temperatures are varied systematically.  
423 The pioneering work of Sarvas (1972) led for example to the triangular temperature response  
424 (peaking at 3.5°C) proposed for the rate of dormancy release (Fig. S3).

425

#### 426 4.3.2 Statistical inference

427       When the experimental approach is not feasible, either because the organism cannot be  
428 reared or cultivated under controlled conditions, or because the physiological state cannot be  
429 determined precisely (e.g. endodormancy or diapause), one can use field or experimental  
430 observations together with meteorological data gathered at the same location to infer model  
431 parameters statistically. Most phenology models have been developed this way.

432       The easiest method consists in fixing all but one parameter to a given value, and finding  
433 the value of the free parameter that minimizes the sum of squared residuals. All parameters are  
434 varied this way one after the other. This technique has several limits, most importantly (i) it is  
435 time consuming, (ii) a finite number of parameter values can be tested, (iii) parameter values  
436 are estimated independently from each other although they are usually not independent, (iv) the  
437 least squares function may have several local optima and it is almost impossible to find the  
438 global optimum without a more thorough search (especially when several parameters are cross-  
439 correlated). Despite the availability of more efficient methods, it seems that in practice  
440 phenology parameters are still estimated with this method, especially in agronomy (Nissanka  
441 et al. 2015), probably because is it quite complex to couple a dynamic crop model to statistical  
442 optimization software.

443       More efficient methods consist in estimating all parameters simultaneously using  
444 optimization algorithms. Traditional optimization algorithms such as downhill simplex or

445 Newton methods (Press et al. 1989) rarely converge towards the global optimum because of the  
446 strong interdependency of phenology model parameters (Kramer 1994). The simulated  
447 annealing method is more effective in this respect (Chuine et al. 1999) because it is especially  
448 designed for functions with multiple optima. More recently, other optimization algorithms have  
449 been used to calibrate phenology models such as the Uniform Covering by Probabilistic Region  
450 (UCPR) (Román-Paoli et al. 2000), and complex maximum likelihood approaches in models  
451 of processes with “hidden states” in arthropods (e.g. Gray et al. 2001; Speybroeck et al. 2006).  
452 Bayesian approaches have also been used to parameterize phenology models, and when coupled  
453 with experimental approaches that provide prior information on the distribution of model  
454 parameters, they have proved powerful (Thorsen & Höglind 2010; Fu et al. 2012)

455

#### 456 **4.4 Model validation**

457 As phenology models must predict future phenology, whether over the coming year (e.g.,  
458 for crop and pest management) or over the next century (e.g., for global warming impact  
459 assessment), accurate parameter estimation is not sufficient, prediction accuracy is also critical.  
460 Cross-validation is an adequate testing method (Chatfield 1988) by which the model is tested  
461 by comparing its predictions to observations not used in model fitting. However, this method is  
462 data-hungry and it is not always possible to split the dataset into two parts, one to fit the model,  
463 the other to test its prediction accuracy. In such case, one can resort to “leave one out” (or  
464 jackknife) cross-validation (Stone 1977).

### 465 **5 Shortcomings of process-based phenology models**

#### 466 **5.1 Parameter estimation: lessons from the statistical approach**

467 As explained earlier, model parameters cannot always be measured under controlled  
468 condition, and statistical inference may be the only way to estimate them. Besides, statistical

469 inference probably appears very appealing as it is quick and it makes good use of long time  
470 series of phenological observations in various countries and therefore climatic conditions.  
471 However, this approach has some shortcomings that should be known. First, some parameters  
472 can be strongly correlated (e.g. base temperature of a GDD and the critical sum to reach  $S^*$ )  
473 which can lead to several statistically equivalent sets of parameters as a whole with however  
474 very different parameter estimates when compared individually. Second, parameter estimation  
475 is dependent on the data used to fit the parameters which represent only a subset of the climatic  
476 conditions encountered by the species/variety across its range (phenological data rarely cover  
477 the entire geographic range of species) and/or its life (long term data series rarely exceed 20  
478 years which is very short compared to the life expectancy of a tree). This can lead to biased  
479 parameter estimates that can become especially problematic when using the models to provide  
480 forecast under future climatic conditions (Lobo 2016).

481         Because of these shortcomings, it is highly recommended not to rely solely on goodness  
482 of fit statistics to choose parameter sets, but also on the shape of the response functions  
483 obtained, as some might be completely unrealistic. Information on the realism of function's  
484 shape comes from the experimental approach. However, recent studies have compared the  
485 phenology of plants and animals under controlled conditions and *in natura*, and found  
486 sometimes substantial differences (Nagano et al. 2012; but see Satake et al. 2013), so that  
487 models parameterized with the experimental approach might perform worse in nature and vice  
488 versa. This suggests that either the effect of some factors or interactions between factors or the  
489 daily variation of these factors in nature might be poorly represented under controlled  
490 conditions, and that epigenetic or acclimation effects might interfere. Therefore, a combination  
491 of both the experimental approach and the statistical approach is probably the best solution to  
492 obtain accurate and realistic models. In applying models derived from controlled-condition  
493 experiments, it is often useful to calibrate model output by comparison with a subset of field

494 observations, modifying the values of one or a few key parameters before validation (e.g.  
495 Régnière et al. 2012a).

## 496 **5.2 Estimating uncertainties**

497 Several sources of uncertainty can arise in predictions of phenological events occurrence:  
498 uncertainty on (i) the hypotheses mathematically formalized in the model (model structure  
499 uncertainty), (ii) the parameter estimates, (iii) model error and of course (iv) weather inputs.  
500 Some studies have used the differences between models as an indication of the model structure  
501 uncertainty (Nissanka et al. 2015, Wallach et al. 2017). Very few studies tried to estimate  
502 parameter estimate uncertainty (Forkel 2014; Alderman & Stanfill 2017). One reason for that  
503 is that statistical methods used so far to estimate parameters did not provide an easy way to  
504 calculate confidence intervals. However, there are various ways to estimate parameter  
505 uncertainty of phenology models. When parameters are estimated by least squares, the variance-  
506 covariance matrix of the parameter estimators can be approximated using second derivatives of  
507 the model with respect to the parameters (Wallach et al. 2016). When a Bayesian approach is  
508 used, the posterior distribution of the estimated parameter vector is a direct result of the  
509 estimation method. Some authors have also proposed to simplify and linearize models  
510 whenever possible in order to use standard R packages (nlme) for parameter estimation and  
511 parameter variance estimation (Nissanka et al. 2015). Finally, model error is usually estimated  
512 by hindcasting or cross-validation.

## 513 **5.3 The current Achilles' heel of process-based phenology models**

### 514 *Geographic variation in parameters*

515 Because process-based phenology models describe how environmental factors affect  
516 adaptive physiological processes, their parameters are supposed to vary among individuals,  
517 among populations/varieties and among species. As phenological traits are highly adaptive  
518 (Chuine 2010; Donohue et al. 2015; Seebacher et al. 2015), we know that local adaptation does

519 exist for these traits (O'Brien et al. 2011; Alberto et al. 2013). Therefore, phenology models  
520 deployed at the scale of a species range should use differentiated parameter estimates across  
521 the range. Very few studies have considered this issue so far (but see Chuine & Beaubien 2001)  
522 as it requires large scale phenology databases to obtain parameter estimates for different  
523 populations. Moreover, combination of different parameter sets to obtain spatially continuous  
524 projections is not straightforward as no one knows either the grain of local adaptation, or how  
525 genetic differentiation varies spatially across a species' range. Data comparing thermal  
526 responses or their genetic correlates across latitudinal gradients would be most useful (e.g.  
527 Bentz et al. 2001).

528

### 529 *Acclimation and plasticity*

530 In animal phenology, there is a growing body of literature focusing on the distinction  
531 between acute and acclimated thermal responses. Most experiments are performed under  
532 constant temperature regimes, where the physiology of the organisms may optimize  
533 development at the temperature they are kept at, through a process called "acclimation"  
534 (Stillman 2003), where the responses to temperature fluctuations differ depending on the  
535 average living conditions of the organism. In general, development times under variable  
536 temperature conditions are shorter than expected from models derived from data collected at  
537 constant temperature, even taking into full account the non-linearity of thermal responses  
538 (Niehaus et al. 2012). This reduction in sensitivity to temperature through physiological  
539 acclimation is expected to reduce the impact of climate change on the performance of species,  
540 especially those living near their upper physiological critical temperature (Seebacher et al.  
541 2015). Surprisingly, few studies on plants have addressed this issue. Most have dealt with the  
542 acclimation of photosynthesis to light (Walters 2005) and temperature (Hikosaka et al. 2006),  
543 but none has addressed the acclimation of developmental rate to temperature or light per se.

544 However, a few studies investigated the effect of daytime vs nighttime temperature on bud  
545 developmental rate (e.g. Rossi & Isabel 2016), which is probably related to the growing body  
546 of evidence of the interplay between photoperiod and temperature in regulating transcriptomic  
547 factors of cell elongation (Sidaway-Lee et al. 2010).

548 The impact of acclimation seems to be more important in aquatic systems and in  
549 environments where natural temperature variability is lower (at lower latitudes), and less in  
550 some taxa (such as arthropods) than in others (such as molluscs) (Seebacher et al. 2015). In a  
551 study specific to the *Drosophila* genus (Insecta: Muscidae), Sorensen et al. (2016) concluded  
552 that plasticity of upper thermal limits was slight, slow to evolve, and that acclimation is weakly  
553 correlated with latitude and thermal variability of the environment. One element of this  
554 discussion seems central however: the precision with which the critical thermal minimum and  
555 maximum are measured (as defined in Stillman 2003). Measuring those thermal thresholds  
556 poses problems because of excessive mortality and inability of organisms to complete critical  
557 developmental steps (such as hatch of molts). More accurate values can be obtained by using  
558 variable temperature regimes coupled with appropriate statistical analysis methods (Régnière  
559 et al. 2012b).

560

### 561 *Modelling rest*

562 Rest is the ultimate synchronizer of seasonality in species that live in extratropical  
563 climates. Understanding the environmental control of rest is crucial to the development of  
564 phenology models in a large number of species, as it represents an adaptation to the cold (or  
565 dry) season (Kozłowski & Pallardy 2002; Hand et al. 2016).

566 Diapause in animals and endodormancy in perennial plants are very complex processes  
567 that have mostly been treated as a black-box or often eluded in modelling (Hodek 1996; Chuine  
568 et al. 2013), mainly because it is difficult to find a good biological indicator of

569 diapause/endodormancy termination on which to base models (e.g. Speybroeck et al. 2006;  
570 Chuine et al. 2016). In many species, the end of diapause/endodormancy and the start of  
571 quiescence/ecodormancy overlap so that “diapause/endodormancy never ends” and the  
572 transition between diapause/endodormancy and quiescence/ecodormancy is gradual (Hänninen  
573 1990; Hodek 1996). So far, a molecular or physiological marker of diapause/endodormancy  
574 break is lacking (Cooke et al. 2012). However, the molecular and genetic mechanisms involved  
575 in diapause/endodormancy induction, maintenance and termination are under intense  
576 investigation and our understanding of this complex process is rapidly evolving (van der Schoot  
577 & Rinne 2011; Xiongbing et al. 2015; Hand et al. 2016; Kang et al. 2016). We foresee the use  
578 of molecular or physiological markers of developmental transitions such as endodormancy for  
579 high throughput phenotyping in the near future, methods that would be most useful for tracking  
580 these dynamic processes during experiments under controlled or natural conditions (Kudoh  
581 2016).

582         The best example of modelling the dynamics of diapause is the work of Gray et al. (2001),  
583 which has allowed simulation of its seasonality over vast landscapes (Régnière et al. 2009). Jia  
584 et al. (2016) use diapause induction by photoperiod and temperature as a critical factor in their  
585 successful seasonal dynamics model of the Asian tiger mosquito *Aedes albopictus* (Skuse)  
586 (Insecta: Diptera; Culicidae). Some models take diapause into direct account in predicting  
587 seasonality (Ridsdill-Smith et al. 2005) model the induction of summer diapause in the  
588 redlegged earth mite *Halotydeus destructor* (Tucker) (Arthropoda: Acari; Penthaleidae)  
589 through a combination of photoperiod and duration of the long-term plant growth season.  
590 Photoperiodic induction of diapause is often mediated by temperature (Saunders 2014).

591         Process-based models of bud endodormancy have so far relied on very little information  
592 about its exact environmental control and have not changed substantially since the pioneering  
593 work of Sarvas (1972), with however the important concept of growth competency introduced

594 by Hänninen (1990). Endodormancy is supposed to be broken after a certain period of exposure  
595 to chilling temperature and response functions to temperature classically show an optimum  
596 between -5°C and 15°C and are either symmetrical or asymmetrical. However, recent advances  
597 in molecular and cell biology, especially regarding the role of 1,3 β glucan in downregulating  
598 cell activity, could provide new insights for modelling endodormancy (van der Schoot & Rinne  
599 2011; Singh et al. 2016).

600 In plants, another important rest period, especially for annuals, is seed dormancy. It is a  
601 complex process with several stages (primary dormancy gradually disappears over time and is  
602 followed by secondary dormancy after a period of low dormancy) with cues and responses to  
603 these cues varying largely among species. Process-based models of germination and seedling  
604 emergence of plants do exist since the 1990s (see review by Forcella et al. 2000), but most have  
605 been developed for weeds (Burghardt et al. 2015, but see MidMore et al. 2015). Simpler  
606 versions of these models rely solely on the hydrothermal time concept, i.e. cumulated time  
607 exposure to soil temperature and soil water potential above specific thresholds. The major  
608 challenge therefore lies in the ability to accurately simulate soil temperature and water potential  
609 (Bullied et al. 2014). To achieve more complex dormancy models, one would also need to take  
610 into account the impact of seed burial depth, oxygen deficiency, light quality, chilling, diurnal  
611 soil temperature fluctuations and maternal environment (epigenetic effects) (Forcella et al.  
612 2000).

613

#### 614 *Modelling photoperiod sensitivity*

615 Plant and animal phenology is dependent on photoperiod, although sensitivity to this cue  
616 varies greatly among species. The photoperiodic cue is linked to the physiology of the circadian  
617 clock (Petterle et al. 2013; Meuti & Denlinger 2013). Photoperiod can interact in a complex  
618 manner with temperature, for example altering the critical photophase, the incidence of

619 diapause, the time of reproduction in insects (Fantinou et al. 2004); and leaf senescence  
620 (Fracheboud et al. 2009), dormancy release (Considine & Considine 2016) and cell elongation  
621 rate in plants (Caffarra et al. 2011a).

622 Regulation of development time by photoperiod has been incorporated in phenology  
623 models long ago, noticeably through the use of a fixed calendar date as a starting point for post  
624 diapause or bud ontogenesis (Chuine et al. 2013), or simple but unsubstantiated relationships  
625 (Kramer 1994). More realistic representations of its effect in models is very recent (Schaber &  
626 Badeck 2003; Caffarra et al. 2011b), and further efforts are needed to incorporate the recent  
627 advances in molecular and cell biology on the regulation of cell activity by photoperiod in  
628 phenology models (Singh et al. 2016).

## 629 **6 Promising avenues and future challenges**

### 630 **6.1 Gene expression phenology modelling**

631 There is increasing potential to incorporate recent advances in our understanding of  
632 molecular-genetic pathways of environmental regulation of development into phenology  
633 models. Research on model organisms such as *Arabidopsis* or annual crops such as rice have  
634 taken a new turn with the study of environment-dependent gene expression thanks to high-  
635 throughput phenotyping techniques that can be deployed in the field (Nagano et al. 2012; Satake  
636 et al. 2013; Kudoh 2016). Phenology models of gene expression level can now be developed.  
637 For example Nagano et al. (2012) built models of the transcriptional response of rice grown in  
638 the field using climate, developmental age, and genotype as input to a simple linear model to  
639 predict the genome-wide transcriptional response. They also tested the models on plants grown  
640 the following year, in which the environment became substantially warmer, and found that the  
641 models were nonetheless highly predictive for the expression of the majority of the genome.  
642 When the relationship between genes expression levels and key developmental processes is

643 known, more complex models can be developed. For example, Satake et al. (2013) developed  
644 the first model of regulatory dynamics of key flowering-time genes in perennial life cycles.  
645 Such models lie perfectly in the lineage of process-based phenology models and could be seen  
646 as their accomplishment. They are indeed parameterized using controlled laboratory  
647 experiments that measure the temporal dynamics of regulatory transcription factors of cell  
648 activity as they change with environmental conditions. These models describe the system at a  
649 higher level of complexity than classical models that simulate the developmental response  
650 resulting from these conditions. The tour de force in the Satake et al. (2013) study lies in the  
651 fact that their model accurately reproduces the seasonal changes in gene expression, the  
652 corresponding timing of floral initiation and return to vegetative growth after a period of  
653 flowering in complex natural environmental conditions while parameterized under finely  
654 controlled experimental conditions.

655         However, although these models are desirable from a process-based knowledge  
656 acquisition perspective, their development and validation requires a large amount of  
657 experimental information that is so far either unavailable or difficult to gather for most species.  
658 The complexity of such models is thus associated with over-parameterization and the reliance  
659 on large and complicated input data sets. Nevertheless, they represent one of the most promising  
660 avenues to improve the realism, and hopefully the reliability, of phenology models in the  
661 upcoming years.

662         Phenology modelling is probably at a turning point thanks to the advances in high-  
663 throughput phenotypic techniques and in molecular and cellular biology that recently brought  
664 several new insights into the regulation of cell activity and more widely on organism  
665 development. Classical phenology models that simulate developmental processes at the  
666 organism level should be confronted, and probably should incorporate recent models focusing  
667 on events at the molecular, cellular, and tissue levels (Pörtner et al. 2006; Chew et al. 2014). A

668 future challenge thus probably lies in combining various modelling techniques (molecular-  
669 level, system-level and biophysical models), which requires a greater coordination between  
670 modellers and biologists and more knowledge transfer between them.

## 671 **6.2 Merging models from different trophic levels: towards community dynamics**

672 The shifts in the phenology of plants and animals worldwide due to global climate change  
673 lead to alterations in phenological synchrony that can have important ecological consequences  
674 at the scale of populations, communities, ecosystems and food webs. For example, the timing  
675 of early spring development plays a key role in plant–herbivore interactions in extratropical  
676 regions and can influence insect performance, outbreak dynamics and plant damage  
677 (Pureswaran et al. 2015). The alteration of the synchrony of leaf unfolding of dominant vs  
678 understory trees can change the competitive balance between them. The alteration of the  
679 synchrony of the flowering and emergence of pollinators alter the reproductive success of plants  
680 and the survival of pollinators. While we are aware of the massive desynchronization of annual  
681 cycles of interacting species because of global climate change (Johansson et al. 2015), there has  
682 so far been very little effort put into modelling multi-species phenology. Pioneer studies in this  
683 field have concerned predator-prey systems (Godfray et al. 1994). Ongoing research also  
684 concerns plant-fungal pathogen synchronization (Marcais & Desprez-Loustau 2014). Other  
685 ongoing research is aimed at modelling the phenology of multispecies systems, either within or  
686 between trophic levels. We can thus foresee that the deficiency of studies in this field will soon  
687 be filled, which will also open new perspectives to study the eco-evolutionary consequences of  
688 phenological asynchrony (Johansson et al. 2015; Pureswaran et al. 2015).

## 689 **6.3 Other future challenges for plant and animal phenology models**

690 One of the greatest challenges for both plant and animal phenology relates to the  
691 geographic variation of thermal response parameters within species, how these patterns develop

692 (Asbury & Angilletta 2010), and how fast they can respond to climate change (de Jong & van  
693 der Have 2009; Donohue et al. 2015).

694         Assessing and taking into account the phenomenon of acclimation in dampening the  
695 effect of changing environmental conditions is also of central importance in plant and animal  
696 phenology modelling (Stillman 2003).

697         We identified two additional future challenges specific to plant phenology models. First,  
698 the vast majority of studies on plants have dealt with leaf unfolding and flowering phenology  
699 (spring events), while leaf senescence and fruit maturation phenology (autumn events) have  
700 been largely neglected despite their ecological importance (Gallinat et al. 2015). A large effort  
701 is now needed to develop reliable phenology models for autumn events (but see Delpierre et al.  
702 2009a). One of the difficulties lies in the lower quality of autumn phenology data, as classical  
703 observation techniques rely on color changes which are very difficult to assess for the human  
704 eye. This difficulty can be partly solved by using new instrumental techniques such as cameras  
705 or radiation sensors allowing an automated detection of color change (Yang et al. 2014).  
706 However, progress in this direction will also involve experimental efforts to identify the  
707 environmental determinants of autumn phenology and its regulation pathways. Here again,  
708 advances in molecular and cellular biology on the regulation of cell activity will be of major  
709 help.

710         Second, we would like to highlight that plant models, used either in agronomy, forestry,  
711 or biogeosciences would certainly gain in realism and accuracy by modelling not only leaf  
712 phenology, but also flower/fruit, cambium, root phenology, and more generally better represent  
713 the timing of the carbon, water and energy fluxes (Richardson et al. 2012; Delpierre et al. 2016).  
714 Timing of these fluxes probably plays an important role in understanding carbon allocation,  
715 growth patterns, seed production and mortality events.

## 716 **7 Conclusion**

717 In this paper, we review considerable evidence of strong convergence in the annual  
718 cycles of plants and ectotherms of extratropical regions, and in their environmental control.  
719 This strong convergence probably depicts common biophysical constraints to life in these  
720 regions, and common adaptation strategies to these constraints. Yet, there has so far been little  
721 cross-fertilisation of plant and animal phenology modelling approaches Plant phenology  
722 modellers could learn greatly from animal phenology modellers to take into account  
723 microclimate variation as well as individual variation in their simulations. Animal phenology  
724 models could also definitely profit from the increasing knowledge of gene expression in  
725 simulating complex processes such as dormancy. Finally, both research communities could  
726 certainly learn from each other to advance our understanding of the mechanisms of  
727 developmental timing, especially regarding rest induction, release and depth.

## 728 **Acknowledgments**

729 The authors are very grateful to Johanna Schmitt for her constructive comments on the  
730 manuscript.

## 731 **Disclosure statement**

732 The authors are not aware of any affiliations, memberships, funding, or financial holdings that  
733 might be perceived as affecting the objectivity of this review.

734

735

736 **Literature Cited**

- 737 Alberto FJ, Aitken SN, Alia R, Gonzalez-Martinez SC, Hänninen H, et al. 2013. Potential for  
738 evolutionary responses to climate change evidence from tree populations. *Glob. Chang.*  
739 *Biol.* 19(6):1645–61
- 740 Alderman PD, Stanfill B. 2017. Quantifying model-structure- and parameter-driven  
741 uncertainties in spring wheat phenology prediction with Bayesian analysis. *Eur. J.*  
742 *Agron.* In press
- 743 Anderson JJ, Gugarie E, Bracis C, Burke BJ, Laidre KL. 2013. Modeling climate change  
744 impacts on phenology and population dynamics of migratory marine species. *Ecol.*  
745 *Model.* 264:83-97
- 746 Asbury DA, Angilletta MJ Jr. 2010. Thermodynamic effects on the evolution of performance  
747 curves. *Am. Nat.* 176:E40-9
- 748 Basler D. 2016. Evaluating phenological models for the prediction of leaf-out dates in six  
749 temperate tree species across central Europe. *Agric. For. Meteorol.* 217:10–21
- 750 Bentz BJ, Logan LA, Vandygriff JC. 2001. Latitudinal variation in *Dendroctonus ponderosae*  
751 (Coleoptera: Scolytidae) development time and adult size. *Can. Entomol.* 133:375-87
- 752 Bratzel F, Turck F. 2015. Molecular memories in the regulation of seasonal flowering: from  
753 competence to cessation. *Genome Biol.* 16(1):192
- 754 Brown JH, Gillooly JF, Allen AP, Savage VM, West GB. 2004. Toward a metabolic theory of  
755 ecology. *Ecology* 85:1771-89
- 756 Bullied WJ, Bullock PR, Flerchinger GN, Acker RC Van. 2014. Agricultural and Forest  
757 Meteorology Process-based modeling of temperature and water profiles in the seedling  
758 recruitment zone : Part II . Seedling emergence timing. *Agric. For. Meteorol.* 188:104–

759           20

760   Burghardt LT, Metcalf CJE, Wilczek AM, Schmitt J, Donohue K. 2015. Modeling the  
761       Influence of Genetic and Environmental Variation on the Expression of Plant Life  
762       Cycles across Landscapes. *Am. Nat.* 185(2):212–27

763   Caffarra A, Donnelly A, Chuine I, Jones MB. 2011a. Modelling the timing of *Betula*  
764       pubescens budburst. I. Temperature and photoperiod: a conceptual model. *Clim. Res.*  
765       46(2):147–57

766   Caffarra A, Donnelly A, Chuine I. 2011b. Modelling the timing of *Betula pubescens* budburst.  
767       II. Integrating complex effects of photoperiod into process-based models. *Clim. Res.*  
768       46(2):159–70

769   Candy SG. 1991. Modeling insect phenology using ordinal regression and continuation  
770       models. *Environ. Entomol.* 20:190-5

771   Charrier G, Ngao J, Saudreau M, Améglio T. 2015. Effects of environmental factors and  
772       management practices on microclimate, winter physiology, and frost resistance in trees.  
773       *Front. Plant Sci.* 6(April):1–18

774   Chatfield C. 1988. *Problem Solving: A Statistician Guide*. London: Chapman & Hall

775   Chew YH, Smith RW, Jones HJ, Seaton DD, Grima R. 2014. Mathematical Models Light Up  
776       Plant Signaling. *The Plant Cell.* 26:5–20

777   Chuine I. 2010. Why does phenology drive species distribution? *Philos. Trans. R. Soc.*  
778       *London Ser. B-Biological Sci.* 365:3149–60

779   Chuine I, Beaubien E. 2001. Phenology is a major determinant of temperate tree range. *Ecol.*  
780       *Lett.* 4(5):500–510

781   Chuine I, Bonhomme M, Legave J-M, Garcia de Cortazar-Atauri I, Charrier G, et al. 2016.  
782       Can phenological models predict tree phenology accurately in the future? The  
783       unrevealed hurdle of endodormancy break. *Glob. Chang. Biol.* 22(10):3444–60

784 Chuine I, Cour P, Rousseau DD. 1999. Selecting models to predict the timing of flowering of  
785 temperate trees: implications for tree phenology modelling. *Plant Cell Environ.*  
786 22(1):1–13

787 Chuine I, Garcia de Cortazar-Atauri I, Kramer K, Hänninen H. 2013. Plant Development  
788 Models. In *Phenology: An Integrative Environmental Science*, ed. MD Schwarz, pp.  
789 275–93. Dordrecht, Netherlands: Springer,. 2nd ed.

790 Colinet H, Sinclair BJ, Vernon P, Renault D. 2015. Insects in fluctuating thermal  
791 environments. *Ann. Rev. Entomol.* 60:123-40

792 Considine MJ, Considine JA. 2016. On the language and physiology of dormancy and  
793 quiescence in plants. *J. Exp. Bot.* 67(11):3189–3203

794 Cooke JEK, Weih M. 2005. Nitrogen storage and seasonal nitrogen cycling in *P. opulus* :  
795 bridging molecular physiology and ecophysiology. *New Phytol.* 167:19–30

796 Cooke JEK, Eriksson ME, Junttila O. 2012. The dynamic nature of bud dormancy in trees:  
797 Environmental control and molecular mechanisms. *Plant, Cell Environ.* 35(10):1707–28

798 Dahlin KM, Fisher RA, Lawrence PJ. 2015. Environmental drivers of drought deciduous  
799 phenology in the Community Land Model. *Biogeosciences.* 12:5061–74

800 de Jong G, van der Have TM. 2009. Temperature dependence of development rate, growth  
801 rate and size: from biophysics to adaptation. In *Phenotypic plasticity of insects:*  
802 *Mechanisms and consequences*, Whitman DW, Ananthakrishnan TN (eds), pp. 523-88,  
803 Science Publishers, Enfield, NH

804 de Reaumur RAF. 1735. Observations du thermomètre, faites à Paris pendant l’année 1735,  
805 comparées avec celles qui ont été faites sous la ligne, à l’isle de France, à Alger et  
806 quelques unes de nos isles de l’Amérique. *Mem. Paris Acad. Sci.* 1735. 545 ff:

807 DeAngelis DL, Grimm V. 2014. Individual-based models in ecology after four decades.  
808 *F1000Prime Reports* 6:39, DOI: [10.12703/P6-39](https://doi.org/10.12703/P6-39)

809 Delisle J, Royer L, Bernier-Cardou M, Bauce E, Labrecque A. 2009. The combined effect of  
810 photoperiod and temperature on egg dormancy in an island and mainland population of  
811 the hemlock looper, *Lambdina fiscellaria*. *Entomol. Exp. Appl.* 133:232-43

812 Delpierre N, Dufrêne E, Soudani K, Ulrich E, Cecchini S, et al. 2009a. Modelling  
813 interannual and spatial variability of leaf senescence for three deciduous tree species in  
814 France. *Agric. For. Meteorol.* 149(6):938–48

815 Delpierre N, Soudani K, Francois C, Kostner B, Pontailier JY, et al. 2009b. Exceptional  
816 carbon uptake in European forests during the warm spring of 2007: a data-model  
817 analysis. *Glob. Chang. Biol.* 15(6):1455–74

818 Delpierre N, Vitasse Y, Chuine I, Guillemot J, Bazot S, et al. 2016. Temperate and boreal  
819 forest tree phenology : from organ-scale processes to terrestrial ecosystem models. *Ann.*  
820 *For. Sci.* 73:5–25

821 Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK et al. 2008. Impacts of  
822 climate warming on terrestrial ectotherms across latitude. *Proc. Natl. Acad. Sci.*  
823 105:6668-72

824 Donohue K, Burghardt LT, Runcie D, Bradford KJ, Schmitt J. 2015. Applying developmental  
825 threshold models to evolutionary ecology. *Trends Ecol. Evol.* 30(2):66–77

826 Duman, J. G. 2001. Antifreeze and ice nucleator proteins in terrestrial arthropods. *Ann. Rev.*  
827 *Physiol.* 63:327-57

828 Duputié A, Rutschmann A, Ronce O, Chuine I. 2015. Consequences of phenological plasticity  
829 for range width and niche breadth of temperate tree species under current and future  
830 climates. *Glob. Chang. Biol.* 21:3062–75

831 Fantinou AA, Perdikis DC, Zota KF. 2004, Reproductive responses to photoperiod and  
832 temperature by diapausing and non-diapausing populations of *Sesamia nonagrioides*  
833 Lef. (Lepidoptera - Noctuidae). *Physiol. Entomol.* 29:169-75

834 Forcella F, Benech Arnold RL, Sanchez R, Ghera CM. 2000. Modeling seedling emergence.  
835 *F. Crop. Res.* 67(2):123–39

836 Forkel M, Carvalhais N, Schaphoff S, Bloh W, Migliavacca M, et al. 2014. Identifying  
837 environmental controls on vegetation greenness phenology through model – data  
838 integration. *Biogeosciences*. 11:7025–50

839 Fracheboud Y, Luquez V, Björkén L, Sjödin A, Tuominen H, Jansson S. 2009. The control of  
840 autumn senescence in European aspen. *Plant Physiol.* 149(4):1982–91

841 Fu YH, Campioli M, Van Oijen M, Deckmyn G, Janssens IA. 2012. Bayesian comparison of  
842 six different temperature-based budburst models for four temperate tree species. *Ecol.*  
843 *Modell.* 230:92–100

844 Gallinat AS, Primack RB, Wagner DL. 2015. Autumn, the neglected season in climate change  
845 research. *Trends Ecol. Evol.* 30(3):169–76

846 Godfray HCJ, Hassel MP, Holt RD. 1994. The population dynamics consequences of  
847 phenological asynchrony between parasitoids and their hosts. *J. Anim. Ecol.* 63:1-10

848 Gray DR, Ravlin FW, Braine JA. 2001. Diapause in the gypsy moth: a model of inhibition  
849 and development. *J. Insect Physiol.* 47:173-84

850 Hand SC, Denlinger DL, Podrabsky JE, Roy R. 2016. Mechanisms of animal diapause: recent  
851 developments from nematodes, crustaceans, insects, and fish. *Am. J. Physiol: Regul.*  
852 *Integr. Comp. Physiol.* 310: R1193-R1211

853 Hänninen H. 1990. Modelling bud dormancy release in trees from cool and temperate regions.  
854 *Acta For. Fenn.* 213:159–65

855 Hänninen H, Kramer K. 2007. A framework for modelling the annual cycle of trees in boreal  
856 and temperate regions. *Silva Fenn.* 41(1):167–205

857 Hikosaka K, Ishikawa K, Borjigidai A, Muller O, Onoda Y. 2006. Temperature acclimation of  
858 photosynthesis: Mechanisms involved in the changes in temperature dependence of  
859 photosynthetic rate. *J. Exp. Bot.* 57(2 SPEC. ISS.):291–302

860 Hodek I. 1996. Diapause development, diapause termination and the end of diapause. *Eur. J.*  
861 *Entomol.* 93:475-87

862 Hogg EH, Price DT, Black TA. 2000. Postulated feedbacks of deciduous forest phenology on  
863 seasonal climate patterns in the western Canadian interior. *J. Clim.* 13:4229–43

864 Jaworski T, Hilszczanski J. 2013. The effect of temperature and humidity changes on insect  
865 development and their impact on forest ecosystems in the context of climate change.  
866 *For. Res. Pap.* 74:345-355.

867 Jia P, Lu L, Chen X, Chen J, Guo J, Yu X, Liu Q. 2016. A climate-driven mechanistic  
868 population model of *Aedes albopictus* with diapause. *Parasites and Vectors* 9:175-90

869 Johansson J, Kristensen NP, Nilsson J-Å, Jonz N. 2015. The eco-evolutionary consequences  
870 of interspecific phenological asynchrony – a theoretical perspective. *Oikos.* 124:102–12

871 Kang DS, Cotton MA, Denlinger DL, Sim C. 2016. Comparative transcriptomics reveals key  
872 gene expression differences between diapausing and nondiapausing adults of *Culex*  
873 *pipiens*. *PLoS One* 11:e0154892

874 Kingsolver JG. 2009. The well-temperated biologist. *Am. Nat.* 174:755-68

875 Knies JI, Kingsolver JG. 2010. Erroneous Arrhenius: modified Arrhenius model best explains  
876 the temperature dependence of ectotherm fitness. *Am. Nat.* 176:227-33

877 Koenig WD, Liebhold AM. 2013. Avian predation pressure as a potential driver of periodical  
878 cicada cycle length. *Am. Nat.* 181:145-9

879 Kogan M. 1998. Integrated pest management: historical perspective and contemporary  
880 developments. *Ann. Rev. Entomol.* 43:1-243

881 Kozłowski TT, Pallardy SG. 2002. Acclimation and adaptive responses of woody plants to

882 environmental stresses. *Bot. Rev.* 68(2):270–334

883 Kramer K. 1994. Selecting a model to predict the onset of growth of *Fagus sylvatica*. *J. Appl.*  
884 *Ecol.* 31:172–81

885 Kudoh H. 2016. Molecular phenology in plants: In natura systems biology for the  
886 comprehensive understanding of seasonal responses under natural environments. *New*  
887 *Phytol.* 210(2):399–412

888 Lang GA, J.D. Early, Martin GC, Darnell RL. 1987. Endo-, para-, and ecodormancy:  
889 physiological terminology and classification for dormancy research . *Hortscience*.  
890 22:371–377

891 Lobo JM. 2016. The use of occurrence data to predict the effects of climate change on insects.  
892 *Curr. Opin. Insect Sci.* 17:62-8

893 Logan JA. 1988. Toward an expert system for development of pest simulation models.  
894 *Environ. Entomol.* 17:359-76

895 Logan JA, Régnière J, Powell JA. 2003. Assessing the impacts of global warming on forest  
896 pest dynamics. *Front. Ecol. Environ.* 1:130-7

897 Maino JL, Kong JD, Hoffman AA, Barton MG, Kearny MR. 2016. Mechanistic models for  
898 predicting insect responses to climate change. *Curr. Opin. Insect Sci.* 17:81-6

899 Marçais B, Desprez-Loustau ML. 2014. European oak powdery mildew : impact on trees ,  
900 effects of environmental factors , and potential effects of climate change. *Ann. For. Sci.*  
901 71:633–42

902 Meuti ME, Denlinger DL. 2013. Evolutionary link between circadian clocks and  
903 photoperiodic diapause in insects. *Integr. Comp. Biol.* 53:131-43

904 Midmore EK, McCartan SA, Jinks RL, Cahalan CM. 2015. Using thermal time models to  
905 predict germination of five provenances of silver birch (*Betula pendula* Roth) in  
906 southern England. *SILVA Fenn.* 49(2):1266

- 907 Misson L, Degueldre D, Collin C, Rodriguez R, Rocheteau A, et al. 2011. Phenological  
908 responses to extreme droughts in a Mediterranean forest. *Glob. Chang. Biol.*  
909 17(2):1036–48
- 910 Moustakas A, Evans ER. 2013. Integrating evolution into ecological modelling:  
911 accommodating phenotypic changes in agent-based models. *PLoS One* 8:e71125
- 912 Murillo-Rincón AP, Kolter NA, Laurila A, Orizaola G. 2017. Intraspecific priority effects  
913 modify compensatory responses to changes in hatching phenology in an amphibian. *J.*  
914 *Anim. Ecol.* 86:128-35
- 915 Mutke S, Ordo JG, Liment JC, Il LG. 2003. Shoot growth and phenology modelling of grafted  
916 Stone pine ( *Pinus pinea* L .) in Inner Spain. *Ann. For. Sci.* 60:527–37
- 917 Nagano AJ, Sato Y, Mihara M, Antonio BA, Motoyama R, Itoh H. 2012. Theory Deciphering  
918 and Prediction of Transcriptome Dynamics under Fluctuating Field Conditions. *Cell.*  
919 151(6):1358–69
- 920 Niehaus AC, Angiletta MJ, Sears MW, Franklin CE, Wilson RS. 2012. Predicting the  
921 physiological performance of ectotherms in fluctuating thermal environments. *J. Exp.*  
922 *Biol.* 215:694-701
- 923 Nissanka SP, Karunaratne AS, Perera R, Weerakoon WMW, Thorburn PJ, Wallach D. 2015.  
924 Environmental Modelling & Software Calibration of the phenology sub-model of  
925 APSIM-Oryza : Going beyond goodness of fit. *Environ. Model. Softw.* 70:128–37
- 926 O’Brien C, Bradshaw WE, Holzappel CM. 2011. Testing for causality in covarying traits:  
927 genes and latitude in a molecular world. *Molec. Ecol.* 20:2471-2476
- 928 Olsson C, Bolmgren K, Lindström J, Maria A. 2013. Performance of tree phenology models  
929 along a bioclimatic gradient in Sweden. *Ecol. Modell.* 266:103–17
- 930 Palacio, S.; Hester, A. J.; Maestro M. MP. 2013. Simulated browsing affects leaf shedding  
931 phenology and litter quality of oak and birch saplings. *TREE Physiol.* 33(4):438–45

- 932 Parton WJ, Logan JA. 1981. A model for diurnal variation in soil and air temperature. *Agric.*  
933 *Meteorol.* 23:205-16
- 934 Petherle A, Karlberg A, Bhalerao RP. 2013. Daylength mediated control of seasonal growth  
935 patterns in perennial trees. *Curr. Opin. Plant Biol.* 16(3):301–6
- 936 Pörtner HO, Bennett AF, Bozinovic F, Clarke A, Lardies MA, Lucassen M, Pelster B,  
937 Schiemer F, Stillman JH. 2006. Trade-offs in thermal adaptation: The need for a  
938 molecular to ecological integration. *Physiol. Biochem. Zool.* 79:295-313
- 939 Powell JA , Logan JA. 2005. Insect seasonality: circle map analysis of temperature-driven  
940 life cycles. *Theor. Popul. Biol.* 67: 161-79
- 941 Press WH, Flannery BP, Teukolsky SA, Vetterling WT. 1989. *Numerical Recipes in Pascal.*  
942 Cambridge: Cambridge University Press
- 943 Pureswaran DS, De Grandpré L, Paré D, Taylor A, Barrette M, Morin H, Régnière J  
944 Kneeshaw D. 2015. Climate-induced changes in host-insect phenology may drive  
945 ecological state-shift in boreal forests. *Ecology* 96:1480-91
- 946 Redaubo F, Le Rouzic A, Dupas S, Silvain J-F, Harry M, Dangles O. 2013. SimAdapt: an  
947 individual-based genetic model for simulating landscape management impacts on  
948 populations. *Methods Ecol. Evol.* 4:595-600
- 949 Régnière J, Powell JA. 2013. Animal life cycle models (Poikilotherms). In *Phenology: An*  
950 *integrative Environmental Science*, Schwartz MD (Ed), pp. 295-315, Springer,  
951 Dordrecht, The Netherlands, Second Edition
- 952 Régnière J, Nealis V, Porter K. 2009. Climate suitability and management of the gypsy moth  
953 invasion into Canada. *Biol. Invasions* 11:135-48
- 954 Régnière J, St-Amant R, Duval P. 2012a. Predicting insect distributions under climate change  
955 physiological responses: spruce budworm as an example. *Biol. Invasions* 14:1571-86
- 956 Régnière J, Powell J, Bentz B, Nealis V. 2012b. Effects of temperature on development,

957 survival and reproduction of insects: Experimental design, data analysis and modeling.  
958 *J. Insect Physiol.* 58:634-47

959 Régnière J, Bentz BJ, Powell JA, St-Amant R. 2015. Individual-based modeling: Mountain  
960 pine beetle seasonal biology in response to climate. In *Simulation modeling of forest*  
961 *landscape disturbances*, Perera AH, Sturtevant BR, Buse LJ (Eds.), pp. 135-164,  
962 Springer, Dordrecht, The Netherlands

963 Ridsdill-Smith J, Pavri C, De Boer E, Kriticos D. 2005. Predictions of summer diapause in the  
964 redlegged earth mite, *Halotydeus destructor* (Acari: Penthaleidea), in Australia. *J. Insect*  
965 *Physiol.* 51:717-26

966 Richardson AD, Anderson RS, Arain MA, Barr AG, Bohrer G, et al. 2012. Terrestrial  
967 biosphere models need better representation of vegetation phenology: results from the  
968 North American Carbon Program Site Synthesis. *Glob. Chang. Biol.* 18(2):566–84

969 Richardson AD, Keenan TF, Migliavacca M, Ryu Y, Sonnentag O, Toomey M. 2013. Climate  
970 change, phenology, and phenological control of vegetation feedbacks to the climate  
971 system. *Agric. For. Meteorol.* 169:156–73

972 Román-Paoli E, Welch S., Vanderlip R. 2000. Comparing genetic coefficient estimation  
973 methods using the CERES-Maize model. *Agric. Syst.* 65(1):29–41

974 Rossi S, Isabel N. 2016. Bud break responds more strongly to daytime than nighttime  
975 temperature under asymmetric experimental warming. *Glob. Chang. Biol.* 1–9

976 Sarvas R. 1972. Investigations on the annual cycle of development on forest trees active  
977 period. *Commun. Instituti For. Fenn.* 76(3):110

978 Satake A, Kawagoe T, Saburi Y, Chiba Y, Sakurai G, Kudoh H. 2013. Forecasting flowering  
979 phenology under climate warming by modelling the regulatory dynamics of flowering-  
980 time genes. *Nat. Commun.* 4:2303

- 981 Saunders DS. 2014. Insect photoperiodism: effects of temperature on the induction of insect  
982 diapause and diverse roles for the circadian system in the photoperiodic response.  
983 *Entomol. Sci.* 17:25-40
- 984 Schaber J, Badeck FW. 2003. Physiology-based phenology models for forest tree species in  
985 Germany. *Int. J. Biometeorol.* 47(4):193–201
- 986 Schoolfield RM, Sharpe PJH, Magnuson CE. 1981. Non-linear regression of biological  
987 temperature-dependent rate models based on absolute reaction-rate theory. *J. Theor.*  
988 *Biol.* 88:719-31
- 989 Schramski JR, Dell AI, Grady JM, Sibly RM, Brown JH. 2015. Metabolic theory predicts  
990 whole-ecosystem properties. *Proc. Natl. Acad. Sci.* 112:2617-22
- 991 Seebacher F, White CR, Franklin CE. 2015. Physiological plasticity increases resilience of  
992 ectothermic animals to climate change. *Nat. Clim. Change* 5:61-6
- 993 Seehausen ML, Régnière J, Martel V, Smith SM. 2017. Developmental and reproductive  
994 responses of the spruce budworm (Lepidoptera: Tortricidae) parasitoid *Tranosema*  
995 *rostrale* (Hymenoptera: Ichneumonidae) to temperature. *J. Insect Physiol.* 98:38-46
- 996 Sidaway-Lee K, Josse EM, Brown A, Gan Y, Halliday KJ, et al. 2010. SPATULA links  
997 daytime temperature and plant growth rate. *Curr. Biol.* 20(16):1493–97
- 998 Singh RK, Svystun T, AlDahmash B, Jönsson AM, Bhalerao RP. 2016. Photoperiod- and  
999 temperature-mediated control of phenology in trees - a molecular perspective. *New*  
1000 *Phytol.* 511–24
- 1001 Soltani A, Hammer GL, Torabi B, Robertson MJ, Zeinali E. 2006. Modeling chickpea growth  
1002 and development: Phenological development. *F. Crop. Res.* 99(1):1–13
- 1003 Sorensen JG, Kritensen TN, Overgaard J. 2016. Evolutionary and ecological patterns of  
1004 thermal acclimation capacity in *Drosophila*: is it important for keeping up with climate

1005 change? *Curr. Opin. Insect Sci.* 17:98-104

1006 Speybroeck N, Lindsey PJ, Billiouw M, Madder M, Lindsey JK, Berkvens DL. 2006.

1007 Modeling diapause termination of *Rhipicephalus appendiculatus* using statistical tools

1008 to detect sudden behavioral changes and time dependencies. *Environ. Ecol. Stat.* 13:69-

1009 87

1010 Sporleder M, Tonnang HEZ, Carhuapoma P, Gonzales JC, Juarez H, Kroschel J. 2013. Insect

1011 Life Cycle Modeling (ILCYM) software a new tool for Regional and Global Insect Pest

1012 Risk Assessments under Current and Future Climate Change Scenarios. In *Potential*

1013 *invasive pests of agricultural crops*, Peña JE (ed). CABI, Boston

1014 Stillman JH.2003. Acclimation capacity underlies susceptibility to climate change. *Science*

1015 301:65

1016 Stoks R, De Block M, Van de Meutter F, Johansson F. 2005. Predation cost of rapid growth:

1017 behavioral coupling and physiological decoupling. *J. Anim. Ecol.* 74:708-15

1018 Stone M. 1977. An Asymptotic Equivalence of Choice of Model by Cross-Validation and

1019 Akaike's Criterion. *Journals R. Stat. Soc. B.* 38:44–47

1020 Takahashi K, Koike S. 2014. Altitudinal differences in bud burst and onset and cessation of

1021 cambial activity of four subalpine tree species. *Landsc. Ecol. Eng.* 10(2):349–54

1022 Thorsen SM, Höglind M. 2010. Modelling cold hardening and dehardening in timothy.

1023 Sensitivity analysis and Bayesian model comparison. *Agric. For. Meteorol.*

1024 150(12):1529–42

1025 Tran K, Ylioja T, Billings R, Régnière J, Ayres MP. 2007. Impact of minimum winter

1026 temperatures on the population dynamics of *Dendroctonus frontalis*. *Ecol. Appl.*

1027 17:882-99

1028 van der Schoot C, Rinne PLH. 2011. Dormancy cycling at the shoot apical meristem:

1029 Transitioning between self-organization and self-arrest. *Plant Sci.* 180:120–31

1030 Visser ME, Holleman LJ. 2001. Warmer springs disrupt the synchrony of oak and winter  
1031 moth phenology. *Proc. Biol. Sci.* 268(1464):289–94

1032 Wallach D, Nissanka SP, Karunaratne AS, Weerakoond, W.M.W. Thorburne PJ, Bootef KJ,  
1033 Jones JW. 2017. Accounting for both parameter and model structure uncertainty in crop  
1034 model predictions of phenology: A case study on rice. *Eur. J. Agron.* In press

1035 Walters RG. 2005. Towards an understanding of photosynthetic acclimation. *J. Exp. Bot.*  
1036 56(411):435–47

1037 Warren J, Topping C. 2001. Trait evolution in an individual-based model of herbaceous  
1038 vegetation. *Evol. Ecol.* 15:15-35

1039 Weinberger JH. 1950. Chilling requirements of peach varieties. *Proc. Amer. Soc. Hort. Sci.*  
1040 56:122–28

1041 Wilson KB, Baldocchi D. 2000. Seasonal and interannual variability of energy fluxes over a  
1042 broadleaved temperate deciduous forest in North America. *Agric For Meteorol.* 100:1–  
1043 18

1044 Xiongbing T, Wang J, Hao K, Whitmann DW, Fan Y, Cao G, Zhang Z. 2015. Transcriptomic  
1045 and proteomic analysis of pre-diapause and non-diapause eggs of migratory locust,  
1046 *Locusta migratoria* L. (Orthoptera: Acridoidae). *Molec. Biol. Evol.* 33:2391-2395

1047 Yamanaka T, Melson WA, Uchimura K, Bjornstad ON. 2012. Generation separation in  
1048 simple structured life cycles: models and 48 years of field data on a tea tortrix moth.  
1049 *Am. Nat.* 179: 95-109

1050 Yang X, Tang J, Mustard JF. 2014. Beyond leaf color: Comparing camera-based phenological  
1051 metrics with leaf biochemical, biophysical, and spectral properties throughout the  
1052 growing season of a temperate deciduous forest. *J. Geophys. Res. Biogeosciences.*  
1053 119:181–91

1054 Zohner CM, Benito BM, Svenning J-C, Renner SS. 2016. Day length unlikely to constrain  
1055 climate-driven shifts in leaf-out times of northern woody plants. *Nat. Clim. Chang.*  
1056 6:1120–1123  
1057

1058  
1059  
1060  
1061  
1062  
1063  
1064  
1065  
1066  
1067  
1068  
1069  
1070  
1071  
1072  
1073  
1074  
1075  
1076  
1077  
1078  
1079  
1080  
1081  
1082  
1083  
1084  
1085  
1086  
1087

## Definitions

### Ectotherm

Cold-blooded animal, more precisely one whose body temperature is dependent on external heat, usually from their environment.

### Phenophase

An observable stage or phase in the annual life cycle of a plant or animal that can be defined by a start and end point.

### Endodormancy/Diapause

Physiological state during which general development and metabolism are inhibited by internal factors.

### Ecodormancy/Quiescence

Physiological state during which general development and metabolism are inhibited by external factors (e.g. temperature, photoperiod, water).

### Process-based model

A model formally describing known or hypothetical cause-effect relationships between physiological processes and some driving factors in the environment.

### Boltzmann factor

The Boltzmann factor,  $e^{-E/kT}$ , is the probability of a state of energy  $E$  relative to the probability of a state of zero energy. It is used to describe the influence of temperature in a wide variety of physical processes.

### Voltinism

The number of generations an animal goes through in a calendar year. Univoltine species have exactly one generation per year. Multivoltine species go through more than one generation per year, and semivoltines one generation every two years.

### Circle maps

A mapping of the date of occurrence of a specific event in an animal's life cycle (e.g. egg stage) from one year to the next. These "maps" can be the object of stability analysis, used to determine the resilience of a life history strategy to climatic perturbations caused by year to year temperature fluctuations.

1088 **Side bar 1**

1089 **Relationship between resting stage and frost hardiness**

1090 Rest plays a key role in resistance to frost which is dynamic along the developmental  
1091 cycle and can be induced only if the rest period has been initiated. In insects, the “diapause  
1092 syndrome” involves the elimination of ice-nucleating agents in the body (such as food in the  
1093 gut and large proteins in the hemolymph and tissues), the accumulation cryoprotectants such  
1094 glycol and glycerol using glycogen as a source, and antifreeze proteins, along with elimination  
1095 of water (Duman 2001). The development of cold tolerance through these mechanisms requires  
1096 an interruption of normal developmental physiology. In plants, phenological processes are  
1097 particularly important for frost avoidance either in spring or autumn. Endodormancy induction  
1098 and release, as well as ecodormancy control the exposure of vulnerable organs to frost as they  
1099 determine cold acclimation and deacclimation (Charrier et al. 2015). Plants have different  
1100 strategies to resist ice formation in the tissues among which the production of anti-freeze  
1101 proteins, ice barriers, increased intracellular osmotic potential through the use of low molecular  
1102 weight molecules such as mono- and oligo-saccharides, polyols, amino acids, lipids, and  
1103 macromolecules such as dehydrins. Like in animals, the deployment of these strategies requires  
1104 an interruption of normal developmental physiology.

1105

1106

1107 **Side bar 2**

1108 **Life cycles of plants and animals**

1109           In annual plants and univoltine animals (with a single generation per year), the life cycle  
1110 can be represented as a circle, or a series of concentric circles (Fig. 1). The circular nature of  
1111 animal life cycles has been the subject of interesting mathematical analysis around the theory  
1112 of circle maps (Powell & Logan 2005; Régnière & Powell 2013). Other animal species are  
1113 multivoltine (complete more than life cycle per year). In plants, most tropical annuals and  
1114 perennials belong to this category. Still other animal species require two or more years to  
1115 complete their life cycle. Bi-annual plants belong to this group. The 17-year cicada is perhaps  
1116 the most notorious extreme example among insects, in this case perhaps as an evolutionary  
1117 strategy to avoid heavy predation by birds (Koenig & Liebhold 2013).

1118

1119

1120 **Future Issues**

1121

1122 1. Incorporating recent models focusing on events at the molecular, cellular, and tissue  
1123 levels into classical phenology models simulating developmental processes at the  
1124 organismal level

1125 2. Merging phenology models from different trophic levels to advance towards models of  
1126 population dynamics and community interactions

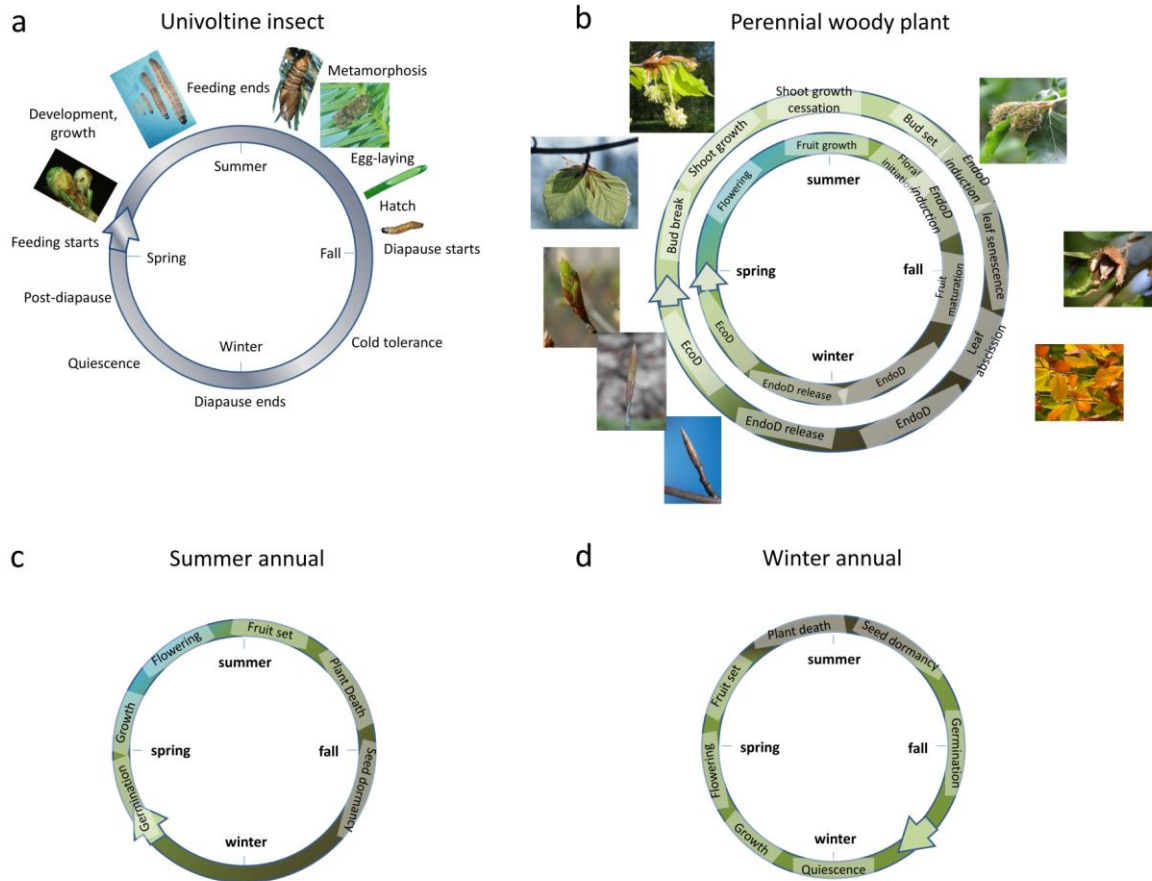
1127 3. Assessing and taking into account geographic variation in developmental parameters  
1128 within species, and how these patterns will be altered by climate change

1129 4. Assessing and taking into account the phenomenon of acclimation in dampening the  
1130 effect of changing environmental conditions

1131 5. Improving autumn phenology models for plants

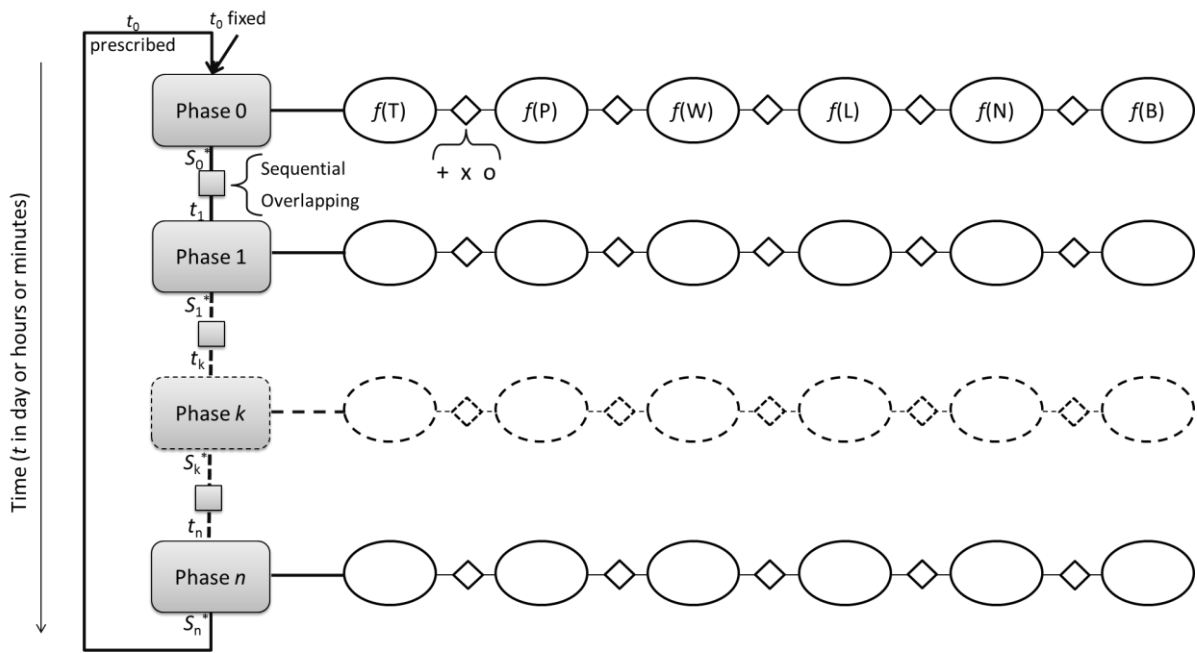
1132 6. Developing integrated phenology models for plants taking into account the phenology of  
1133 all organs (leaves, flowers/fruits, wood, root)

1134



1135  
 1136  
 1137  
 1138  
 1139  
 1140  
 1141  
 1142

**Figure 1.** Animal and plant life cycles are circle maps, in their simplest expression repeating events on an annual basis more or less at the same calendar dates thus constituting circle maps (*sensu* Powell and Logan 2005). To development, other stage-specific processes such as foraging, feeding, predation, reproduction and dispersal, can be linked. (a) univoltine insect (here, the spruce budworm); (b) tree, (c) summer annual plant, (d) winter annual plant.



1143

1144 Figure 2. General overview of a generic process-based phenology model. A model can be seen  
 1145 as a metamodel comprising several submodels, each describing a component of the cycle (a  
 1146 development phase). Development is represented by a state variable,  $S$  for development stage,  
 1147 which is the summation of development over time ( $t$ , in steps of days, hours, or minutes) from  
 1148 a start date, as a function of environmental cues. If the cycle comprises  $n + 1$  development  
 1149 phases (Figure 2), by definition  $S_0 = 0$  at  $t_0$  in the initial stage (e.g., seed germination, egg hatch)  
 1150 and  $S_n$  reaches some maximum value ( $S_n^*$ ) at the end of the last stage (often defining an annual  
 1151 cycle). Each development phase  $k$  starts at time  $t_k$  and ends at time  $t_{k+1}$ , defined by the time  
 1152 when  $S_k$  reaches the value  $S_k^*$ , which is specific to the model. Each development phase is  
 1153 described by a submodel determining its reaction norms  $f$  to various cues ( $T$ , temperature;  $P$ ,  
 1154 photoperiod;  $W$ , water;  $L$ , light;  $N$ , nutrient;  $B$ , stressful biotic interaction). Response functions  
 1155 combine by addition (+), multiplication ( $\times$ ), or composition ( $\circ$ ). Phases either are sequential  
 1156 (follow each other in time) or overlap (one phase can start before the end of the previous phase).  
 1157 Grey boxes represent the development phases. Open ovals represent the response functions to  
 1158 environmental cues. Grey squares represent the modes of phase interaction. Overlapping  
 1159 interaction involves other functions, not represented in the scheme, describing the relationships  
 1160 between either state of development or rate of development between phases. Open diamonds  
 1161 represent the interaction modes between response functions (addition, multiplication,  
 1162 composition).

1163

1164 **Supplemental Material For Process-Based Models of Phenology for plants**  
1165 **and animals**

1166

1167 **Isabelle Chuine<sup>1</sup> & Jacques Régnière<sup>2</sup>**

1168

1169 1 CEFE-CNRS, Montpellier, France, [isabelle.chuine@cefe.cnrs.fr](mailto:isabelle.chuine@cefe.cnrs.fr)

1170 2 Natural Resources Canada, Canadian Forest Service, Québec, Canada,

1171 [jacques.regniere@canada.ca](mailto:jacques.regniere@canada.ca)

1172

1173

1174 **Content**

1175 I. Supplemental material

1176 S1. Importance of phenology models in environmental sciences modelling

1177 S2. Universal Temperature Dependence of the Metabolic theory of Ecology

1178 S3. Response functions to environmental cues

1179

1180 II. Supplemental Figures

1181 Figure S1. Thermal response typical of animal ectotherms

1182 Figure S2. Distribution of the individual variation in development rate

1183 Figure S3. Main types of functions used to represent the action of temperature (and other

1184 cues) in phenology models

1185

1186 III. Supplemental References

1187

1188 **S1. Importance of phenology models in environmental sciences modelling**

1189           The timing of developmental stages is important in agronomy as it determines the yield  
1190 and the organoleptic quality of the harvest. This is why phenological traits are among the most  
1191 important phenotypes considered in varietal selection. One of the most important differences  
1192 between cultivars is in the times required for accomplishing the various development stages.  
1193 Because many of the major physiological processes depend on development stages, predictions  
1194 of crop models are very sensitive to the accuracy of crop phenology models (Van Oort et al.  
1195 2011), and obtaining acceptable error margins in phenology is critical in crop modelling (Mall  
1196 & Aggarwal, 2002).

1197           The biosphere plays a prominent role in the Earth’s climate dynamics. It has thus  
1198 become essential that Terrestrial Biosphere Models, imbedded into Earth System Models and  
1199 simulating the temporal dynamics of biological processes on land, have an accurate  
1200 representation of vegetation phenology. Yet, to date, existing models are unlikely to predict  
1201 future phenological responses to climate change accurately and will misrepresent the  
1202 seasonality and interannual variability of key biosphere–atmosphere feedbacks and interactions  
1203 (Richardson et al. 2012).

1204           The inclusion of phenology models into population dynamics models dates back to the  
1205 1980s, and concerned mostly the management of insect herbivores. Issues of synchronized  
1206 phenology across trophic levels have more recently become central to understanding the impact  
1207 of climate change on ecosystem functions (Godfray et al. 1994; Pureswaran et al. 2015).  
1208 Phenology and thermal response modelling have widened to cover a variety of systems,  
1209 including aquatic ecosystems (Anderson et al. 2013). Phenology models predict physiological  
1210 responses to multiple dynamic environmental factors. By linking models across successive life  
1211 stages, they predict life cycles and generation times, and form the framework of many  
1212 demographic models.

1213           The key role of the timing of phenological events for reproductive success and survival  
1214 of most multicellular organisms, led phenology models to play a central role in process-based  
1215 distribution models designed either for plants or animals (Chuine et al. 2001; Kearney et al.  
1216 2010; Régnière et al. 2012a). In comparison to correlative species distribution models, process-  
1217 based models offer the possibility to understand the fundamental reasons for the presence or  
1218 absence of a species under particular environmental conditions. They describe the biological  
1219 processes that determine whether a particular organism can or cannot perform adequately under  
1220 on those conditions, altering survival and reproductive success, and ultimately fitness and the  
1221 likelihood of presence.

1222           Because the timing of development is a key component of fitness, phenology models  
1223 can also be used to analyze various processes in evolutionary ecology. It is becoming clear that  
1224 taxonomic variability and strong phylogenetic relationships exist in the strength of thermal  
1225 responses (Irlich et al. 2009; Dell et al. 2011; Huey & Kingsolver 2011). The ability of process  
1226 models to address this variability and evolutionary processes is probably one the most  
1227 promising avenues for further development of ecological niche theory and the metabolic theory  
1228 of ecology (Brown et al. 2004). Yet very few studies have addressed such questions so far  
1229 (Donohue et al. 2015; Duputié et al. 2015; Kearney et al. 2009; Seebacher et al. 2015). But we  
1230 predict that they will become more numerous every year, especially as there is also now  
1231 increasing potential to incorporate information on molecular-genetic pathways of  
1232 environmental regulation of development into these models (Satake et al. 2013).

1233

1234 **S2. Universal Temperature Dependence of the Metabolic theory of Ecology**

1235 The Metabolic Theory of Ecology (MTE) posits that relationships between body mass ( $M$ ),  
1236 temperature ( $T$ , in °K) and rates of biological processes ( $R$ , development, metabolism,  
1237 population growth, ecological interactions at the scale of ecosystems) are simple allometric  
1238 scaling relationships of the type

1239 
$$R = R_0 M^\alpha e^{-(E/kT)} \quad [S1]$$

1240 where  $R_0$  is a proportionality constant,  $\alpha$  is an exponent, expected to be a multiple of 1/4, and  
1241 the term  $\exp(-E/kT)$  is the Boltzmann factor, expected to represent the universal temperature  
1242 dependence (UTD) of chemical as well as biological processes. Within this term,  $E$  is reaction  
1243 activation energy and  $k$  is Boltzmann's constant and  $T$  is absolute temperature in °K. The MTE  
1244 further suggests that the activation energy should be relatively constant, within the range  $E =$   
1245 0.6-0.7 eV.

1246 While the MTE constitutes a highly valuable framework for unifying ecology and  
1247 physiology through fundamental processes, there has been considerable discussion in the  
1248 literature about its details. Several favourable tests of the MTE have been conducted (Bailly et  
1249 al. 2014). But the use of the Boltzmann factor as a valid UTD has been hotly debated (Clarke  
1250 2006; O'Connor et al. 2007; Knies and Kingsolver 2010). The MTE's assertion of a near-  
1251 constant value of activation energy  $E \approx 0.65$  eV across taxa is also controversial. Irlich et al.  
1252 (2009), Dell et al. (2011) and Huey & Kingsolver (2011) found considerably more variation in  
1253 the value of  $E$  than expected from the MTE, much of which was linked to phylogenetic  
1254 relationships and environmental living conditions (mean and variance).

1255 A replacement of the Boltzmann factor can be based on the Eyring equation, at the base  
1256 of transition state theory:

1257 
$$r = K (kT/h) \exp\left[\frac{1}{R}\left(S_A - \frac{H_A}{T}\right)\right] = \sigma T \exp\left[\frac{1}{R}\left(S_A - \frac{H_A}{T}\right)\right] \quad [S2]$$

1258 where  $r$  is the rate of a physiological process,  $K$  is a proportionality constant,  $k$  is Boltzmann's  
 1259 constant,  $h$  is Plank's constant,  $T$  is temperature (°K),  $S_A$  and  $H_A$  are the reaction's entropy  
 1260 and enthalpy of activation, and  $R$  is the gas constant (which is Boltzmann's constant divided  
 1261 by Avogadro's number). The expression can be simplified by defining the constant  
 1262  $\sigma = K(k/h)$ . Equation [S2] has three parameters ( $\sigma$ ,  $S_A$  and  $H_A$ ) that determine the rate of  
 1263 any specific process at temperature  $T$ .

1264 But the Eyring equation still does not account for the unimodal nature of thermal  
 1265 responses. This led to the formulation of the Sharpe & DeMichele (1977) equation, a  
 1266 modification of Eyring's equation [S2] that introduced four additional parameters relating  
 1267 temperature to the proportion of the rate-limiting enzyme that is active:  $S_L$ ,  $S_H$ ,  $H_L$ , and  $H_H$   
 1268 that are changes in entropy ( $S$ ) and enthalpy ( $H$ ) associated with low (index  $L$ ) and high (index  
 1269  $H$ ) temperatures, respectively. The complexity of this equation and the difficulty of obtaining  
 1270 sufficient data to estimate its parameters prompted Schoolfield et al. (1981) to simplify it, and  
 1271 to offer graphical methods for initial parameter estimation. Their modified equation, with its 6  
 1272 parameters, has been widely used since in modelling animal responses to temperature:

$$1273 \quad r(T) = \frac{\rho_{25} \frac{T}{298} \exp\left[\frac{H_A}{R} \left(\frac{1}{298} - \frac{1}{T}\right)\right]}{1 + \exp\left[\frac{H_L}{R} \left(\frac{1}{T_L} - \frac{1}{T}\right)\right] + \exp\left[\frac{H_H}{R} \left(\frac{1}{T_H} - \frac{1}{T}\right)\right]} \quad [S3]$$

1274 where  $T$  is temperature (in °K). The 6 estimable parameters are:  $\sigma_{25}$ , the rate at which a  
 1275 process proceeds at 25°C (298°K),  $H_A$ , the reaction's enthalpy of activation,  $H_L$  and  $T_L$ , and  
 1276  $H_H$  and  $T_H$  that are changes in enthalpy and 50% deactivation temperatures associated with  
 1277 low (index  $L$ ) and high (index  $H$ ) temperatures. Statistical estimation of those parameters  
 1278 requires at least 7 measurements made at different temperatures, including measurements near  
 1279 the denaturation temperatures  $T_L$  and  $T_H$  where survival is often an issue. Similar equations

1280 have been proposed by Fishmann (1987) and Erez (1988) for plant responses to temperature  
1281 during endodormancy.

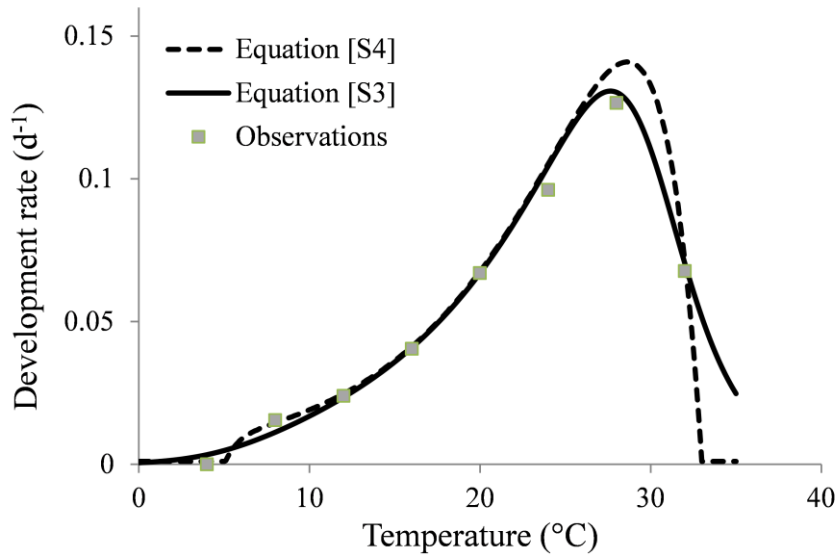
1282 Régnière et al. (2012b) developed an empirical function from previous work to better  
1283 describe thermal responses near lower and upper critical temperatures:

$$1284 \quad r(T) = \psi \left[ e^{\omega(T-T_b)} - \left( \frac{T_m - T}{T_m - T_b} \right) e^{-\omega(T-T_b)/\Delta_b} - \left( \frac{T - T_b}{T_m - T_b} \right) e^{\omega(T_m - T_b) - (T_m - T)/\Delta_m} \right] \quad [S4]$$

1285 valid over the range  $T_b \leq T \leq T_m$  where  $T$  is temperature ( $^{\circ}\text{C}$ ) ( $r(T) = 0$  otherwise).  
1286 Equation [S4] also has 6 estimable parameters, each analogous to a corresponding parameter in  
1287 equation [S3]:  $\psi$  is a proportionality constant (analogous to  $\sigma_{25}$ );  $\omega$  is analogous to  $H_A$ ;  $T_b$   
1288 and  $T_m$  are the lower and upper critical temperature thresholds (analogous  $T_L$  and  $T_H$ ); and  $\Delta_b$   
1289 and  $\Delta_m$  are the range of temperatures over which lower and upper thresholds influence the  
1290 response function (analogous to  $H_L$  and  $H_H$ ). Equations [S3] and [S4] overlap over most of the  
1291 temperature range that leads to development, but differ considerably around the critical  
1292 temperatures (Fig. S1).

1293 The variation of developmental responses between individuals probably stems from  
1294 variation in all parameters of thermal response models (de Jong & van de Have 2009). Régnière  
1295 & Powell (2013) have shown that incorporating all of this variation into a term with log-normal  
1296 distribution and mean 1 as a multiplier of the proportionality constant  $\sigma_{25}$  in equation [S3] or  
1297  $\psi$  in equation [S4] was a very good approximation of observed variability (Fig. S2).

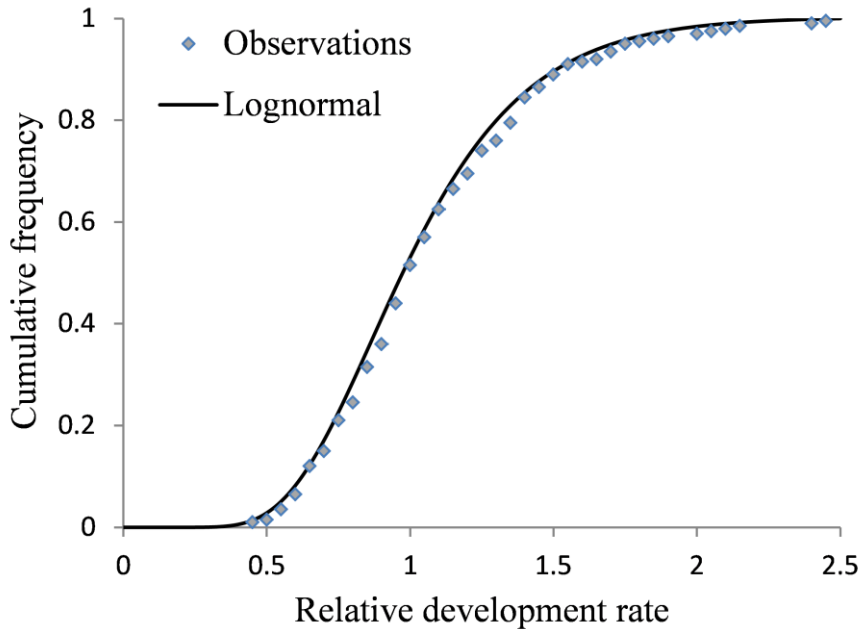
1298



1299

1300  
1301  
1302  
1303  
1304  
1305  
1306

**Figure S1.** Thermal response typical of animal ectotherms, displaying the Eyring-type exponential response in the median range (10-25°C), the optimal temperature ( $T_{opt}$ ) as well as decreasing responses near minimum and maximum critical temperature thresholds ( $T_b$ ,  $\Delta_b$ ,  $T_m$  and  $\Delta_m$ ). Solid line is equation [S3] (Schoolfield et al. 1981), dotted line is equation [S4] (Régnière et al. 2012b).



1307

1308  
1309  
1310  
1311  
1312

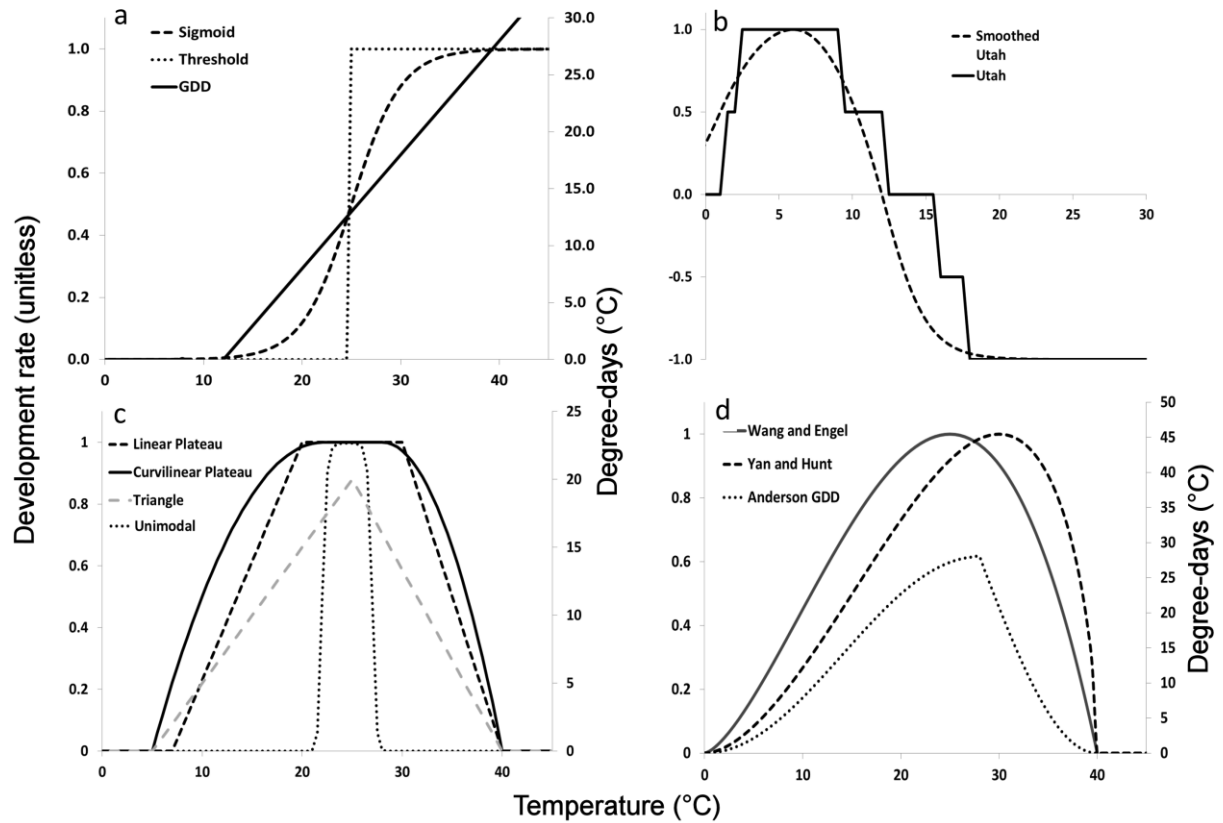
**Figure S2.** Distribution of the individual variation in development rate, relative to the median rate, when all parameters of equations [S3] or [S4] vary between individuals. Solid line: log-normal distribution (after Régnière and Powell 2013).

1313

### S3. Responses functions to environmental cues

1314 Figure S3 illustrates the different types of response functions that have been used to describe  
1315 the developmental response to temperature and photoperiod in plants and animals. Although  
1316 we know from experimental evidence that response functions of cell elongation and growth rate  
1317 are unimodal and asymmetrical (Fig. S3b, d), simpler functions have been used successfully:  
1318 symmetrical unimodal functions (Fig. S3c), linear or non-linear monotonic functions, with  
1319 positive and negative slopes (Fig. S3a). The Utah function and its smoothed variant have been  
1320 used as a response function to temperature during endodormancy of peach flower buds and has  
1321 the particularity to take into account negative effects of warm temperatures on endodormancy  
1322 release, as also does the Dynamic model proposed by Fishman et al. (1987) and Erez et al.  
1323 (1988) but with a different formulation. Monotonic functions have been widely used to describe  
1324 the response to temperature of cell elongation (during ecodormancy of buds and the first phase  
1325 of fruit growth) in plants, while unimodal functions have rather been used to describe the  
1326 response to temperature during endodormancy and the fruit maturation phase in plants as well  
1327 as development rate in insects.

1328



1329

1330 **Figure S3.** Main types of function used to represent the action of temperature (and other cues)  
 1331 in phenology models. (a) monotonic function (either linear or not, here with positive slope, but  
 1332 negative slopes are also used); (b) Utah function and its smoothed version, used initially for  
 1333 peach phenology, has the particularity to represent negative effect (i.e. reversible effect) of  
 1334 temperature at high temperature range; (c) symmetrical unimodal functions; (d) asymmetrical  
 1335 unimodal functions. Functions are illustrated here as functions of temperature, ranging from 0  
 1336 to 40°C, but they have also been used with other variables, e.g. photoperiod.  
 1337

1338

## 1339 **8 Supplementary References**

- 1340 Anderson JJ, Gugarie E, Bracis C, Burke BJ, Laidre KL. 2013. Modeling climate change  
1341 impacts on phenology and population dynamics of migratory marine species. *Ecol.*  
1342 *Model.* 264: 83-97
- 1343 Bailly D, Cassemiro FAS, Agostinho CS, Marques EE, Agostinho AA. 2014. The metabolic  
1344 theory of ecology convincingly explains the latitudinal diversity gradient of Neotropical  
1345 freshwater fish. *Ecology* 95: 553-62
- 1346 Brown JH, Gillooly JF, Allen AP, Savage VM, West GB. 2004. Toward a metabolic theory of  
1347 ecology. *Ecology* 85:1771-89
- 1348 Chuine I, Beaubien E. 2001. Phenology is a major determinant of temperate tree range. *Ecol.*  
1349 *Lett.* 4(5):500–510
- 1350 Clarke A. 2006. Temperature and the metabolic theory of ecology. *Funct. Ecol.* 20: 405-12
- 1351 de Jong G, van der Have TM. 2009. Temperature dependence of development rate, growth  
1352 rate and size: from biophysics to adaptation. In *Phenotypic plasticity of insects:*  
1353 *Mechanisms and consequences*, Whitman DW, Ananthakrishnan TN (eds), pp. 523-88,  
1354 Science Publishers, Enfield, NH Dell AI, Pawar S, Savage VM. 2011. Systematic  
1355 variation in the temperature dependence of physiological and ecological traits. *Proc.*  
1356 *Natl. Acad. Sci.* 108: 10591-6
- 1357 Donohue K, Burghardt LT, Runcie D, Bradford KJ, Schmitt J. 2015. Applying developmental  
1358 threshold models to evolutionary ecology. *Trends Ecol. Evol.* 30:66–77
- 1359 Duputié A, Rutschmann A, Ronce O, Chuine I. 2015. Consequences of phenological plasticity  
1360 for range width and niche breadth of temperate tree species under current and future  
1361 climates. *Glob. Chang. Biol.* 21:3062–75
- 1362 Erez A, Fishman S, Gat Z, Couvillon GA. 1988. Evaluation of winter climate for breaking  
1363 bud rest using the dynamic model. *Acta Hortic.* 232:76–89

- 1364 Fishman S, Erez A, Couvillon GA. 1987. The temperature dependence of dormancy breaking  
1365 in plants: Mathematical analysis of a two-step model involving a cooperative transition.  
1366 *J. Theor. Biol.* 124:473–83
- 1367 Godfray HCJ, Hassel MP, Holt RD. 1994. The population dynamics consequences of  
1368 phenological asynchrony between parasitoids and their hosts. *J. Anim. Ecol.* 63: 1-10
- 1369 Huey RB, Kingsolver JG. 2011. Variation in universal temperature dependence of biological  
1370 rates. *Proc. Natl. Acad. Sci.* 108: 10377-8
- 1371 Irlich UN, Terblanche JS, Blackburn TM, Chown SL. 2009. Insect rate-temperature  
1372 relationships: Environmental variation and the metabolic theory of ecology. *Am. Nat.*  
1373 174: 819-35
- 1374 Kearney M, Porter WP, Williams C, Ritchie S, Hoffmann AA. 2009. Integrating biophysical  
1375 models and evolutionary theory to predict climatic impacts on species' ranges: the  
1376 dengue mosquito *Aedes aegypti* in Australia. *Funct. Ecol.* 23(3):528–38
- 1377 Kearney M, Simpson SJ, Raubenheimer D, Helmuth B. 2010. Modelling the ecological niche  
1378 from functional traits. *Philos. Trans. Royal Soc. B* 365: 3469-83
- 1379 Knies JJ, Kingsolver JG. 2010. Erroneous Arrhenius: modified Arrhenius model best explains  
1380 the temperature dependence of ectotherm fitness. *Am. Nat.* 176: 227-33
- 1381 Mall RK, Aggarwal PK. 2002. Climate change and rice yields in diverse agro environments of  
1382 India. I. Evaluation of impact assessment models. *Clim. Change* 52:315–30
- 1383 O'Connor MP, Kemp SJ, Agosta SJ, Hansen F, Sieg AE, Wallace BP, McNair JN, Dunham  
1384 AE. 2007. Reconsidering the mechanistic basis of the metabolic theory of ecology.  
1385 *Oikos* 116: 1058-72
- 1386 Pureswaran DS, De Grandpré L, Paré D, Taylor A, Barrette M, Morin H, Régnière J  
1387 Kneeshaw D. 2015. Climate-induced changes in host-insect phenology may drive  
1388 ecological state-shift in boreal forests. *Ecology* 96: 1480-91

1389 Régnière J, Powell JA. 2013. Animal life cycle models (Poikilotherms). Phenology: An  
1390 integrative Environmental Science, Schwartz MD (ed.), pp. 295-315, Springer, Second  
1391 Edition

1392 Régnière J, St-Amant R, Duval P. 2012a. Predicting insect distributions under climate change  
1393 physiological responses: spruce budworm as an example. *Biol. Invasions* 14: 1571-86  
1394

1395 Régnière J, Powell J, Bentz B, Nealis V. 2012b. Effects of temperature on development,  
1396 survival and reproduction of insects: Experimental design, data analysis and modeling.  
1397 *J. Insect Physiol.* 58: 634-47

1398 Richardson AD, Anderson RS, Arain MA, Barr AG, Bohrer G, et al. 2012. Terrestrial  
1399 biosphere models need better representation of vegetation phenology: results from the  
1400 North American Carbon Program Site Synthesis. *Glob. Chang. Biol.* 18(2):566–84

1401 Satake A, Kawagoe T, Saburi Y, Chiba Y, Sakurai G, Kudoh H. 2013. Forecasting flowering  
1402 phenology under climate warming by modelling the regulatory dynamics of flowering-  
1403 time genes. *Nat. Commun.* 4:2303

1404 Schoolfield RM, Sharpe PJH, Magnuson CE. 1981. Non-linear regression of biological  
1405 temperature-dependent rate models based on absolute reaction-rate theory. *J. Theor.*  
1406 *Biol.* 88:719-31

1407 Seebacher F, White CR, Franklin CE. 2015. Physiological plasticity increases resilience of  
1408 ectothermic animals to climate change. *Nat. Clim. Change* 5: 61-6

1409 Sharpe PJH, DeMichele DW. 1977. Reaction kinetics of poikilotherm development. *J. theor.*  
1410 *Biol.* 64:649-70

1411 Van Oort PAJ, Zhang T, de Vries ME, Heinemann AB, Meinke H. 2011. Correlation between  
1412 temperature and phenology prediction error in rice (*Oryza sativa* L.). *Agric. For.*  
1413 *Meteorol.* 151:1545–55

