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3
4 **Title**

5 Process-Based Models of Phenology for plants and animals

6
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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 20th 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. 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; Penthalidae)
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.

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734

735

736 **Literature Cited**

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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.

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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).

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1120 **Future Issues**

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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

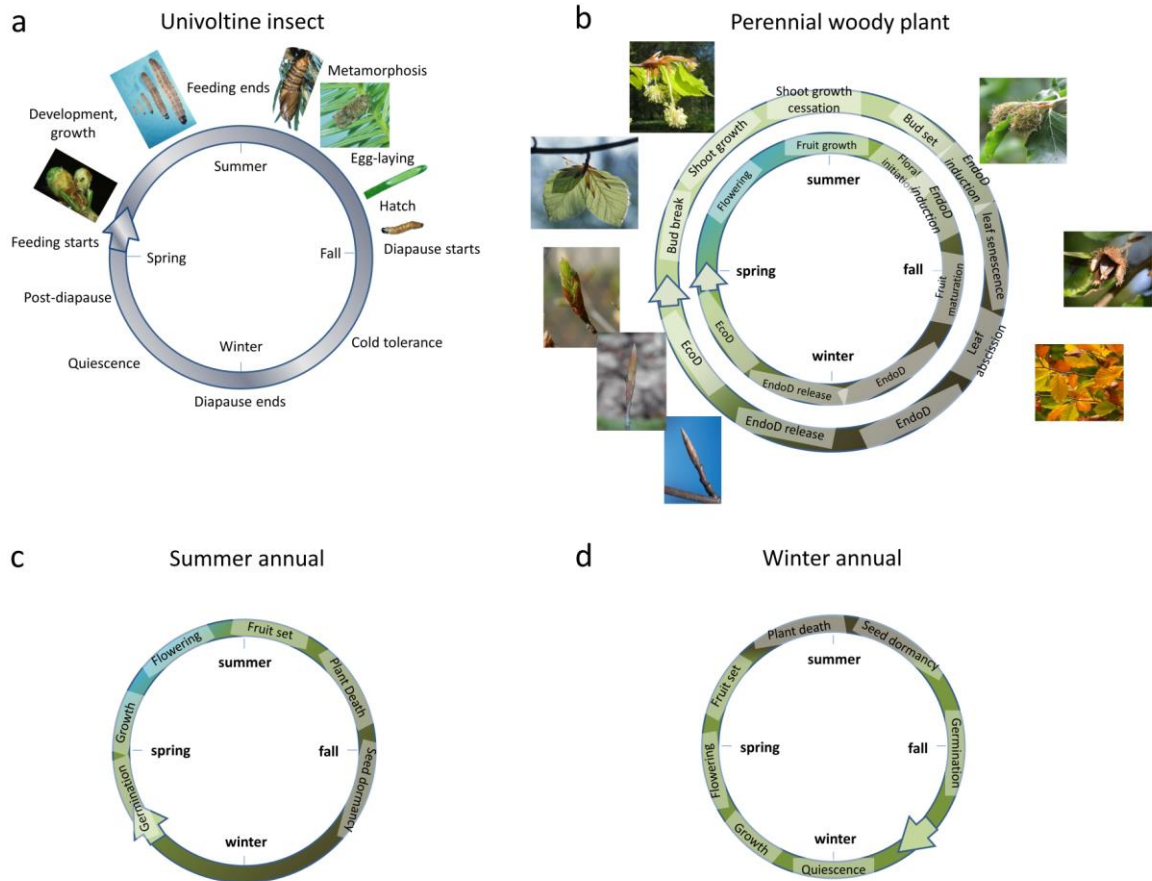
1127 3. Assessing and taking into account geographic variation in developmental parameters
1128 within species, and how these patterns will be altered by climate change

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

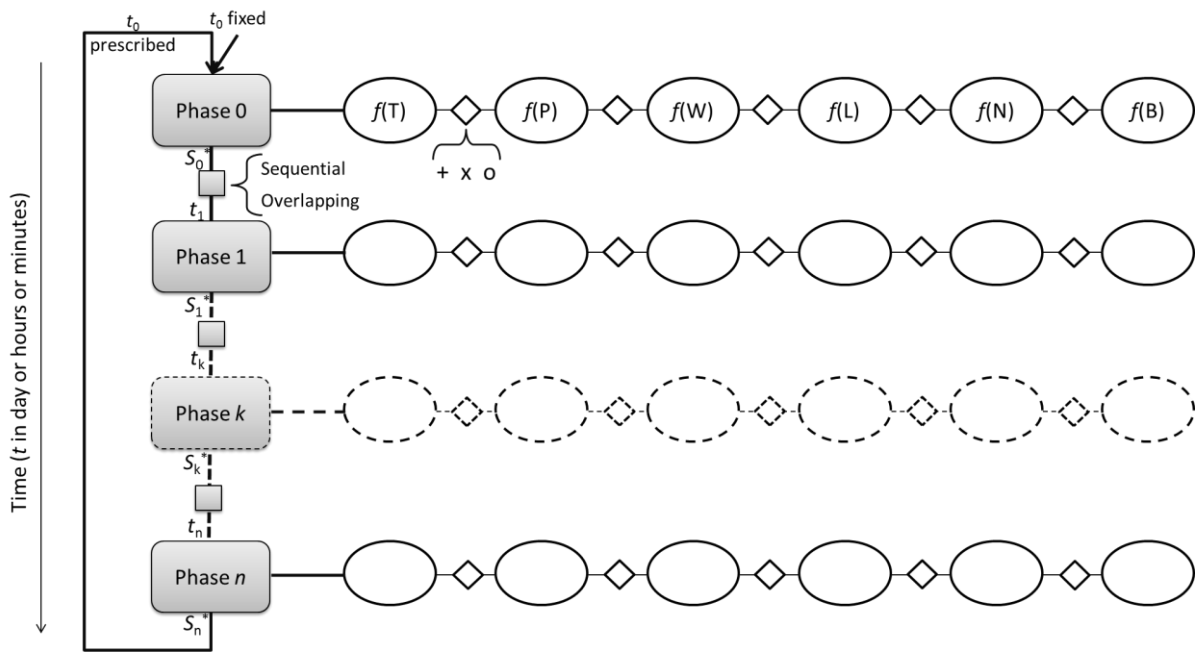
1132 6. Developing integrated phenology models for plants taking into account the phenology of
1133 all organs (leaves, flowers/fruits, wood, root)

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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).

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

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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).

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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, α 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 (σ , 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: σ_{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.

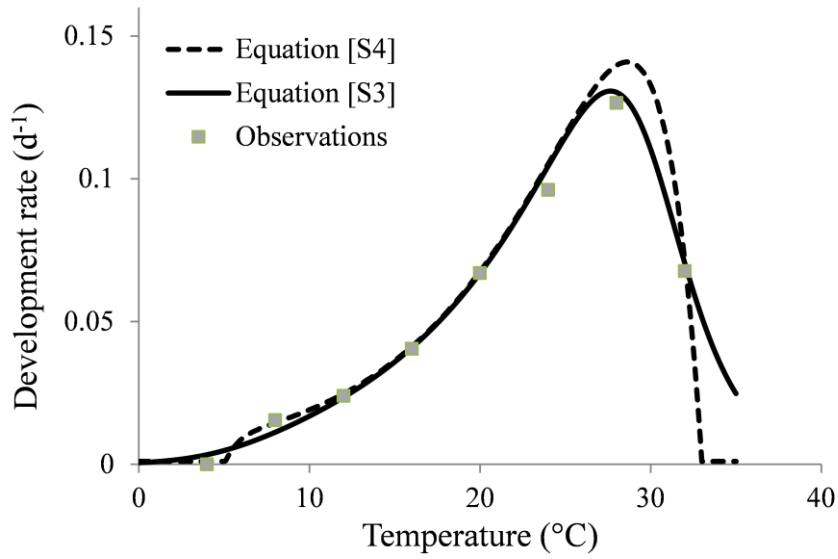
1282 Régnière et al. (2012b) developed an empirical function from previous work to better
1283 describe thermal responses near lower and upper critical temperatures:

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

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]: ψ is a proportionality constant (analogous to σ_{25}); ω 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 Δ_b
1289 and Δ_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 σ_{25} in equation [S3] or
1297 ψ in equation [S4] was a very good approximation of observed variability (Fig. S2).

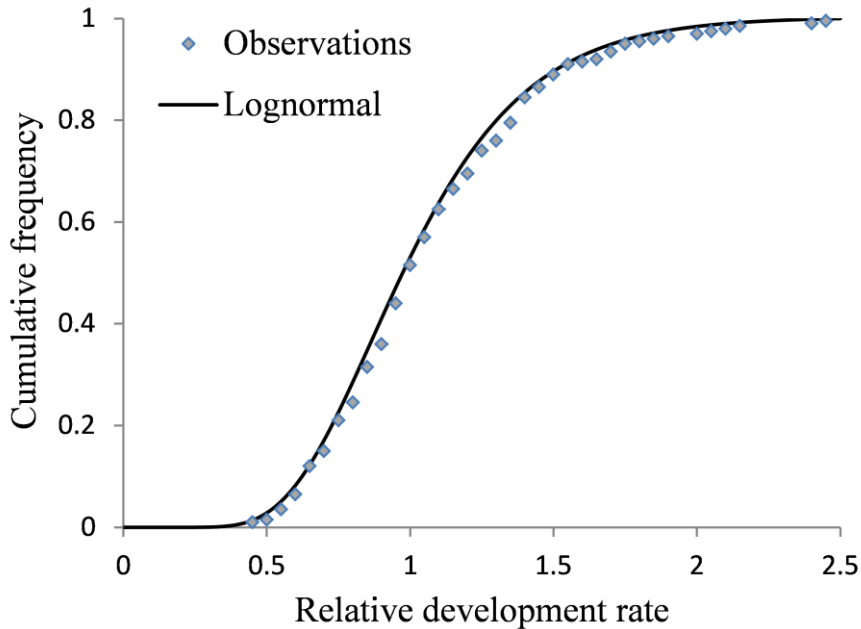
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Figure S1. Thermal response typical of animal ectotherms, displaying the Eyring-type exponential response in the median range (10-25°C), the optimal temperature (T_{opt}) as well as decreasing responses near minimum and maximum critical temperature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



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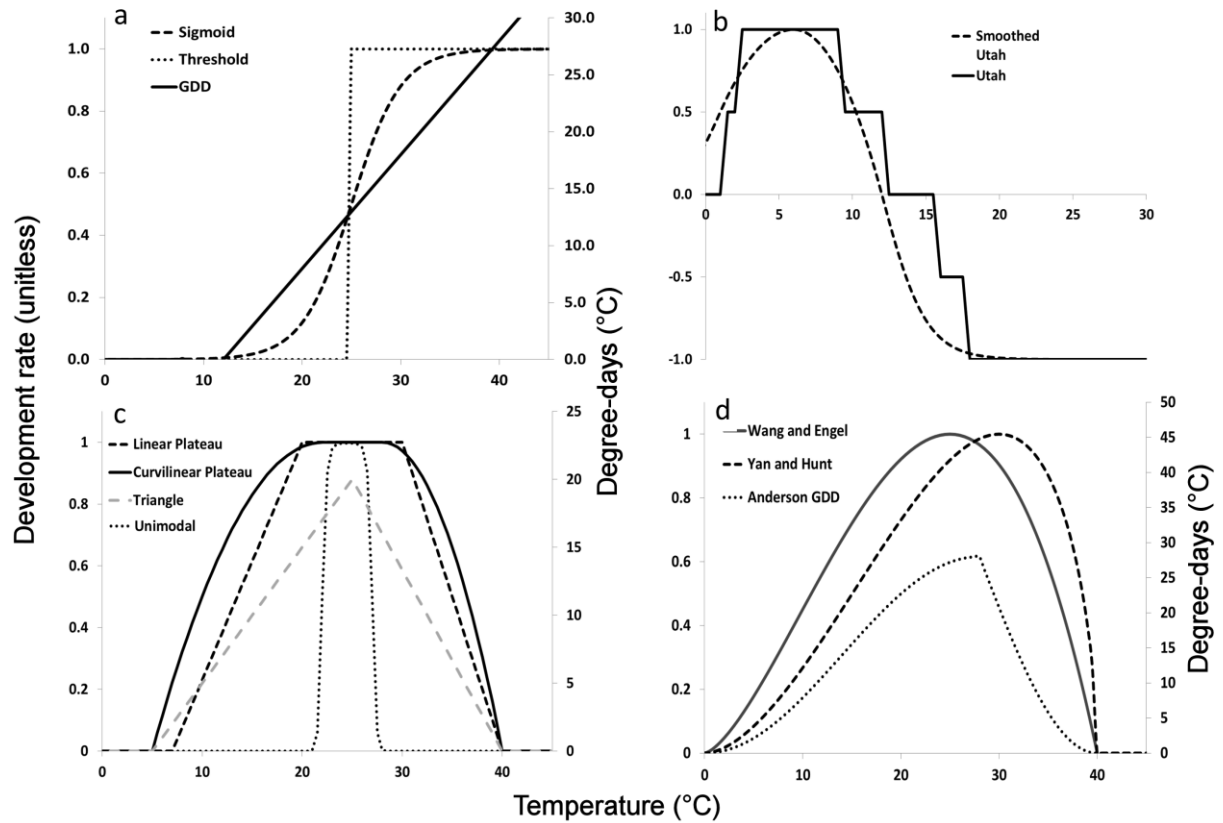
Figure S2. Distribution of the individual variation in development rate, relative to the median rate, when all parameters of equations [S3] or [S4] vary between individuals. Solid line: log-normal distribution (after Régnière and Powell 2013).

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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.

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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.
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