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## Assembling and testing a generic phenological model to predict *Lobesia botrana* voltinism for impact studies.

Victorine Castex, Iñaki García de Cortázar-Atauri, Pierluigi Calanca, Martin Beniston, Jérôme Moreau

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1 *Ecological Modelling*

2

3 **Title: Assembling and testing a generic phenological model to predict *Lobesia Botrana* voltinism**  
4 **for impact studies**

5

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13

14 **Informative title :** A generic model for *L.botrana* voltinism

15

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28 **Abstract:**

29 The physiological development of insect pests is driven by temperature and photoperiod. Geographic  
30 variations in the speed of growth reflect current patterns in thermal conditions as a function of latitude  
31 and altitude. Global warming will likely lead to shifts in pests' phenology. Insects are expected to  
32 overwinter earlier and develop more generations, with implications for the risks of damage to  
33 agricultural crops. Understanding and monitoring of the voltinism of insect pests will be increasingly  
34 important to anticipate critical phases of pest development and devise options for adapting pest control  
35 measures. In this study, we describe a new generic phenological model that allows to reproduce the  
36 voltinism of *Lobesia botrana*, a major insect pest that affect grapevine production (*Vitis vinifera* L.)  
37 worldwide.

38 Inspired by existing models, the Lobesia Generic Model (LGM) combines two submodels representing  
39 the overwintering period and the dates of flight of subsequent generations of male insects. This model  
40 uses a unique Beta function for representing the temperature responses of both the overwintering  
41 generation as well as the adult generations. The results indicate that LGM is able to simulate *L.*  
42 *botrana* voltinism under climatic conditions ranging from those observed in Southern Spain to those  
43 recorded in the Alsace region (France). The LGM only requires a single set of parameters valid for all  
44 the generations with a precision of around 7 days (RMSE), allowing a simple use with parameters  
45 representative of natural behaviour and found in the existing literature.

46 **Keywords:** Generic phenological modelling, *Lobesia botrana*, voltinism, process-based model,  
47 temperature, photoperiod

48

49 **Key Messages**

- 50
- 51 • We present a generic model of *L. botrana* voltinism that assembles existing components
  - 52 • We assume that thermal requirements are the same for all generations, and use one the same  
53 Beta function to represent the temperature response of all generations
  - 54 • We show that the model performs well across sites ranging from Southern Spain to the Alsace  
55 region (France)
- 56

57 **1. Introduction**

58 Modern agriculture relies on the massive use of pesticides to increase productivity (Tilman et al.  
59 2002). This has caused considerable stress on biodiversity and made insect pests more resistant to  
60 pesticides (Hatt et al. 2018). Furthermore, extensive commercial trade as well as increasing

61 temperatures have enhanced the spread of insect pests. As a result, invasive species have started to  
62 damage crops in remote areas (Bale et al. 2002; Lin 2011; Lamichhane et al. 2015). Understanding  
63 and predicting insect pest dynamics is necessary in order to ensure productivity while reducing the use  
64 of chemicals (Bregaglio et al. 2013). In the context of global warming, there is also a need to  
65 understand how pest species dynamics will evolve in the future. In this context, phenological models  
66 are interesting tools to monitor populations dynamics and to predict their evolution, e.g., under  
67 changing environmental and climatic conditions (Steinbauer et al. 2004; Nietschke et al. 2007;  
68 Stoeckli et al. 2012). Such models are capable of anticipating insects' voltinism and allows improving  
69 treatment periods (Moravie et al. 2006).

70 Process-based models aim to represent biological processes through equations that describe  
71 developmental, survival, fecundity or mortality rates for different life-stages of insects (from  
72 prediapause to overwintering). Among the different processes simulated, phenology (development) is  
73 probably one of the most important, because it defines the biological cycle (Chuine et al. 2013).  
74 Insects are ectotherms and consequently their physiological development is mainly driven by  
75 temperature (Zhou et al. 1995; Bale et al. 2002; Tobin et al. 2008). They exhibit a response to thermal  
76 variation (Singer and Parmesan 2010; Bale and Hayward 2010; Brodeur et al. 2013; Moiroux et al.  
77 2014) by adjusting life history traits like the date of overwintering and population growth (Hance et al.  
78 2007; Moreau et al. 2017). Diapause and overwintering are further determined by photoperiod (Pavan  
79 et al. 2006; Svobodová et al. 2014). Both temperature and photoperiod thus explain how insects' life  
80 cycle respond to local climatic conditions, latitude and altitude (Honêk 1996; Ioriatti et al. 2011).  
81 Changes in the growing rate and geographical distribution of pests have already been observed in the  
82 last decades (Baumgärtner et al. 2012) as a consequence of recent changes in climate.

83  
84 Among the numerous species that affect agriculture, *Lobesia botrana* (Den. & Schiff) commonly  
85 named the European grapevine moth, is a good candidate for assessing effects of climate change on  
86 the development of insect pests. It is a major grapevine insect pest that is present worldwide, including  
87 Europe. As a multivoltine species, this pest is able to complete from two (in northern parts of Europe)  
88 to four (in southern parts of Europe) generations per year according to climate and latitude (Martín-  
89 Vertedor et al. 2010). Under warmer conditions it has the potential of generating more damage than  
90 currently, as its development will begin earlier in the season and last longer (Castex et al. 2017;  
91 Marchesini and Monta 2004). The life cycle of *L. botrana* is characterized by its capacity to enter into  
92 diapause at the pupal phase when day length is less than 14 hours (12 hours is the limit for pupal  
93 overwintering). The individuals will overwinter as pupa and start developing before becoming adults  
94 and mate to start their adult life and reproduction cycle (Thiery, 2008).

95

96 Many models have been developed to monitor the adult flights of *L. botrana* (Tab.1). They all can be  
 97 considered as process-based models, despite using different temperature response functions (Caffarra  
 98 et al. 2012; Caffarelli and Vita 1988; Gabel and Mocko 1984; Gallardo et al. 2009; Logan et al. 1976;  
 99 Milonas et al. 2001; Touzeau 1981). Other models adopt a statistical approach to represent biological  
 100 responses to temperature (Moravie et al. 2006).

101  
 102 Existing models for *L. botrana* target different purposes. Some of them describe the growing length at  
 103 different developmental phases (Touzeau 1981; Gabel and Mocko 1984; Caffarelli and Vita 1988;  
 104 Briere and Pracros 1998 and 1999; Severini et al. 2005). Others focus on the timing of maximum moth  
 105 flight (Moravie et al. 2006; Amo-Salas et al. 2011; Ortega-López et al. 2014), forecast the emergence  
 106 timing (Arca et al. 1993; Milonas et al. 2001) and population size (Gallardo et al. 2009), the number of  
 107 generations occurring before diapause (Caffarra et al. 2012) or model the overwintering process  
 108 (Baumgärtner et al. 2012). Finally, very complex models such as that of Gutierrez et al. (2012) try to  
 109 simulate various processes simultaneously (grapevine phenology, adult development, survival and  
 110 fecundity rates).

111  
 112  
 113 **Tab.1**: Comparison between local models and the generic model described in this work. The following  
 114 exhaustive literature review list the existing phenological models for *L. botrana*: (1) Gabel and Mocko 1984; (2)  
 115 Caffarelli and Vita 1988; (3) Arca et al. 1993; (4) Briere and Pracros 1999; (5) Gutierrez et al. 2012; (6) Milonas  
 116 et al. 2001, (7) Severini et al. 2005; (8) Moravie et al. 2006; (9) Gallardo et al. 2009; (10) Amo-Salas et al. 2011,  
 117 (11) Caffarra et al. 2012; (12) Baumgärtner et al. 2012; (13) Ortega-López et al. 2014; (14) Gilioli et al. 2016  
 118  
 119

	Local models (see refs. in the legend)	Lobesia Generic Model described in this study
Input parameters and processes	-Temperature: mean, minimum, maximum, daily, hourly (1; 2; 3; 4; 9; 11; 12) -Relative humidity (10; 13) -Photoperiod (1; 4; 5; 12) -Mortality and growth rates (7)	-Temperature (mean daily) -Photoperiod
Method of calculation	-Accumulation of growing degree-days - Different thermal time requirements according to the generations (1;2;3;6;9;11)	-Accumulation of growing degree-days -Same thermal time requirements to achieve subsequent phases within one generation and for all the generations
Phases modeled	-Prediapause/ Diapause/ Post-diapause (5; 7; 12; 14) -Overwintering (12) -Egg, larval and pupa phases (3; 5; 10; 11) -1 <sup>st</sup> (8; 13), 2 <sup>nd</sup> (6) and 3 <sup>rd</sup> (9) adults flights	-Prediapause/ Diapause/ Post-diapause (overwintering) -Adult flights (10% and 50% of males flights)
Beginning of calculation	-1st January (8; 10; 11; 13) -1st March (6; 9) or 5th March (1) -After diapause induction (DL<14.15h) (5) -Day of overwintering (previous year) (7) -Day of the 1st individual to enter in diapause (12) -End previous generation (chrysalides) (3)	- ( $d_0$ )= -183 (July 15th) corresponding to the day with > 12h of day length in Spain (the most southern site of observed data). The LGM start calculating in late summer (i.e. of the previous year n-1), so for the prediapause.

Type of model	<ul style="list-style-type: none"> <li>-Population / Rate sum model (6; 9; 12)</li> <li>-Empirical / Biologically Based model (1; 3; 4; 6; 10; 11; 13)</li> <li>-Physiologically Based Demographic Model (5; 14)</li> <li>-Aged structure (7)</li> </ul>	- Voltinism Process Based Model with a statistical approach
Strength	<ul style="list-style-type: none"> <li>- Perform well under same conditions as considered during model development</li> <li>- Easy to implement if local data are available</li> <li>- Suitable for integration into Decision Support Tools</li> </ul>	<ul style="list-style-type: none"> <li>- 1 set of parameters</li> <li>- Suitable for large scale impact studies as climate change scenarios</li> </ul>
Weakness	<ul style="list-style-type: none"> <li>- Not necessarily reproducible at other sites with the same parameters (applicability to new situations needs to be verified)</li> <li>- Different sets of parameters for each region, generation and between the phases (based on the analysis of the different models, ESM7).</li> <li>- Local models are not applicable to large scale studies</li> </ul>	-Predictions across sites are robust even if performance quality can be low in specific cases

120

121

122 Irrespective of type, structure and complexity, most of the models given in Tab.1 were developed to  
123 (a) operate at the local scale, implying that they require local sets of parameters (e.g.,: Trentino, Italian  
124 Alps, in Caffarra and Eccel 2011), and (b) to account for possible differences in thermal requirements  
125 between different generations, meaning that parameters are usually specified for each generation  
126 separately (Touzeau 1981; Gabel and Mocko 1984; Caffarelli and Vita 1988; Milonas et al. 2001;  
127 Gallardo et al. 2009; Caffarra et al. 2012). For this reason, some authors have already highlighted the  
128 difficulty of using and comparing these models within a larger range of climatic conditions than  
129 initially targeted (Flores and Azin 2015; Allen 1976; Gallardo et al. 2009; Amo-Salas et al. 2011). In  
130 fact, a major downside with local models is that they need local adjustments when applied outside the  
131 geographic area targeted in first place. To the best of our knowledge, only a few models, such as the  
132 one developed by Baumgärtner et al. (2012) or Ortega-López et al. (2014) have been applied to large  
133 geographical scales.

134

135 The overall purpose of this work is to present a generic model for *L. botrana* (hereafter called Lobesia  
136 Generic Model or LGM) that considers a large scale of application and a single response to  
137 temperature or thermal time requirements for all generations (Tab.1). The model is built by  
138 assembling existing model components and calibrated in such a way as to obtain a generic set of  
139 parameters. Model development and calibration were carried out using PMP, a user-friendly software  
140 providing an interface for designing, setting up, testing and running phenological models (Chuine et  
141 al. 2013).

142

143 The specific aims of this study are 1) to analyze existing models of *L. botrana* voltinism in order to  
144 propose a generic approach for simulating representative phase of development (10% and 50% of the  
145 male flights) of an adult population from diapause to last flight; and 2) to propose a validated standard

146 set of parameters for applications at the large scale. We use for this purpose a large database of flight  
147 observations compiled in a wide latitudinal transect running from southern Spain to northern France  
148 (Fig.1) and representing Mediterranean and Continental climate types (Jongman et al. 2006; Beck et  
149 al. 2018).

150

## 151 **2. Materials and Methods**

### 152 **2.1 Data used in the study**

#### 153 ***2.1.1 Phenological data of *L. botrana****

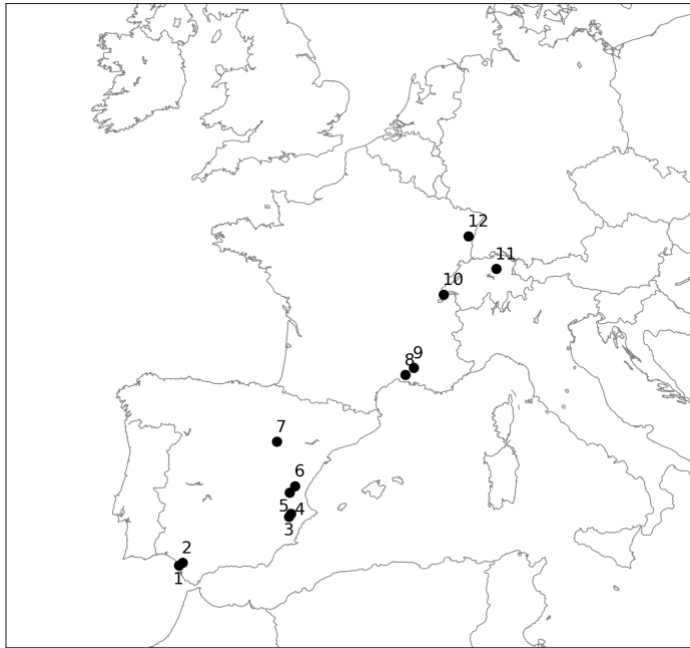
154 The observed data of *L. botrana* correspond to the number of individuals captured per week, by  
155 pheromone (sexual confusion) delta traps placed at the beginning of March. Traps are changed and  
156 counted weekly to represent the distribution of population from the first flight of the first generation  
157 (who overwintered) to the last adult flight of the last generation. Traps are considered one of the best  
158 way to capture and represent male flight activity (Milonas et al. 2001; Gallardo et al. 2009; Ortega-  
159 López et al. 2014). Data were provided by private sector enterprises, inter professional councils in the  
160 agronomical and viticulture sectors and academic institutions (Tab.2). As illustrated in the map  
161 (Fig.1), 12 sites were used to cover latitudes between Lat.36.710°N and Lat.48.213°N and an altitude  
162 range from 0 m a.s.l. (Saint Gilles, France) and 692 m a.s.l. (Requena, Spain). We have assumed that it  
163 was possible to combine all the data from different sites to calibrate and evaluate the model, even if  
164 there is no standardized protocol for the observation of adult flights in trap catches.

165 **Tab.2.** *L. botrana* adult flights data and meteorological data acquisition per site in latitudinal order.

166

Site Number	<i>Lobesia Botrana</i>		Meteorological station				
	Site (data provider)	Years obs	Data provider	Period	Latitude (°N)	Longitude (°E)	Altitude (m a.s.l)
1	Sanlucar (Junta de Andalucia)	2008, 2009, 2015	Jerez de la frontera (Junta de Andalucia)	2007-2015	36.7	-6.1	56
2	Trebujena (Junta de Andalucia)	2013, 2014					
3	Yecla_C_abajo (O. comarcal Agraria de Alahama)	2010, 2011, 2012, 2014, 2015, 2016	Yecla-Pinillos (SIAM)	2007-2017	38.6	-1.1	602
4	Fuente de la Higuera Alforins (Generalitat Valencia)	2012, 2013, 2014, 2015, 2016	Caudete (SIAR)	2010-2017	38.7	-1.0	625
5	Requena Las Monjas (Generalitat Valencia)	2012, 2013, 2014, 2015, 2016	Requena Cerrito - Arcis (SIAR)	2010-2017	39.5	-1.11	692
6	Villar del Arzobispo (Generalitat Valencia)	2012, 2013, 2014, 2015, 2016	Chullilla/ Villar (SIAR Riegos IVIA)	2010-2017	39.3	-0.8	380
7	Cariñena (D.O.P-Vino las piedras)	2011, 2012, 2013, 2014	Calatayud (Sarga)	2004-2016	41.3	-1.6	591
8	Avignon (Chambre Agri. Gard - France)	2005, 2009	Avignon (INRA Climatik)	2003-2016	43.9	4.8	24
9	St Gilles (Chambre Agri. Gard - France)	2015, 2016	St-Gilles (INRA Climatik)	2010-2017	43.7	4.4	0
10	Changins (Agroscope) Switzerland	1997, 1998, 1999, 2000, 2001, 2010	Changins (Meteosuisse IDAWEB)	1997-2017	46.4	6.2	455
11	Eibindinger (Agroscope) Switzerland	2009, 2010, 2011, 2012, 2013, 2014	Staefa (agrometeo Meteosuisse)	2004-2017	47.2	8.7	408
12	Scherwiller (Fredon) Chambre Agri. Alsace - France)	2010, 2011, 2012, 2013, 2016	Bergheim (INRA-Climatik)	2009-2016	48.2	7.4	200





167

168 **Fig.1.** Map of the study sites in Europe (produced with MakeMap from an open source code). The numbers in  
 169 the map represent the study sites introduced in Tab.2.

170 Of the initially 90 records, 51 records of (non consecutive) observations of *L. botrana* adult flight  
 171 (entire cycle of generations) on an annual basis (Tab.2) were retained after quality control. From those  
 172 annual male flights, we identified two main phenological observations: the 10% and 50% of the total  
 173 adult flights per generation as done in Gallardo et al. (2009). To do so, we identified and separated the  
 174 generations of adults as explained in ESM1 (Electronic Supplementary Material). Then, we calculated  
 175 the cumulated sum of the number of individuals caught in the traps, for each generation (G1; G2; G3;  
 176 G4). From this sum, we took the 10% and 50% of the cumulated sum per generation (G1-10%, G1-  
 177 50%; G2-10%, G2-50%; etc.). This data was then related to its corresponding Day Of Year (DOY) of  
 178 observation. The observed data are not continuous in time (from 1997 to 2016), because observations  
 179 are not made systematically. Also, we only used the observed data when we could clearly identify the  
 180 beginning, the peak and the end of the generations that represent around 70% of all the data we  
 181 collected.

182

### 183 **2.1.2 Meteorological data**

184 Meteorological data were obtained from different meteorological services at each site (Tab.2). Daily  
 185 minimum, maximum and mean temperatures were collected from meteorological stations in an array  
 186 with a maximum distance of 10-15 km from the collection sites of *L. botrana* flights, and almost at the  
 187 same altitude as the vineyards, which we considered reasonable for the representation of local  
 188 meteorological conditions.

189

190

191 **2.2. A generic phenological model for *L. botrana***

192 **2.2.1 General description of the model**

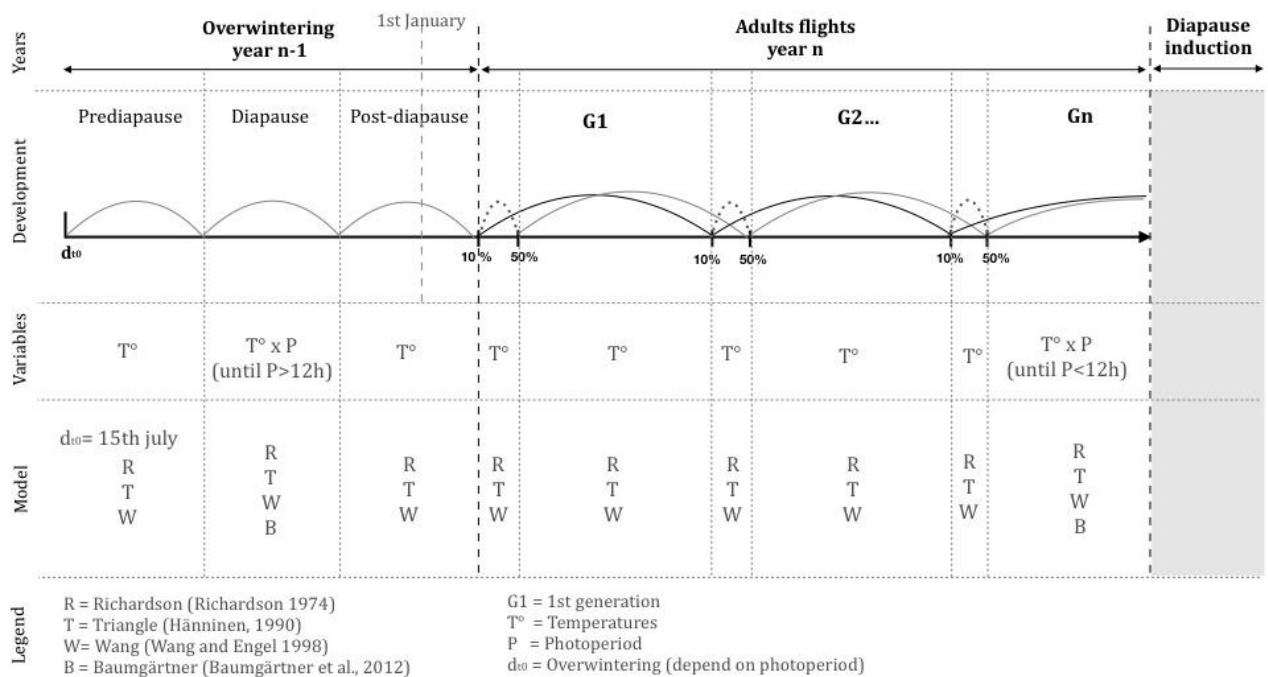
193 The LGM is a combination of two submodels allowing the simulation of at least five phases of  
 194 development representing two development stages (Fig.2): 1) The overwintering submodel: It  
 195 considers three phases, prediapaue, diapause and post diapause from the year n-1 to n; 2) The male  
 196 adult flights submodel: reproduce the 10% and 50% of the total of the population of each generation  
 197 for the year n. At least two generations can be reproduced, with an option for additional generations  
 198 depending on local climatic conditions and latitude.

199 Phase is a specific part in a physiological development process (e.g., in the overwintering stage, we  
 200 identify the prediapaue phase).

201

202 Baumgärtner et al. (2012) propose a complex model to simulate the overwintering stage and the adult  
 203 development (at different phases) considering the speed of growth. In this study, we will only consider  
 204 the first cohort (i.e., the emergence of the first individuals) of each generation (corresponding to our  
 205 10% of flight in Fig.2) considering the accumulation of thermal time.

206



207

208 **Fig. 2.** LGM conceptual modelling framework. This aims at reproducing the overwintering period and the adults  
 209 flights :10%-10% and 50%-50% of flight between generations and the 10% and 50% within a generation itself  
 210 (dotted line). Also the variables used (T°=Temperature and P=Photoperiod) or the functions used in the model  
 211 representing the temperature response: Richardson (R), Triangle (T) and Wang (W) are represented for each  
 212 physiological developmental phase of *L. botrana*.

213

214 The overwintering of *L. botrana* is simulated following Baumgärtner et al. (2012) and Gutierrez et al.  
 215 (2012) i.e. considering three phases.

- 216 1- Prediapause: development depend on temperature
- 217 2- Diapause: development depend on a combination of temperature and photoperiod
- 218 3- Post-diapause: development depend on temperature

219  
 220 The adults flights consider two or more adults generations and depend on temperature and local  
 221 climatic conditions. We propose to simulate the 10% and 50% of the total of the population of each  
 222 generation. The calculation considers the adults that enter into diapause in the previous year (n-1).

223 We apply the following equation to describe the temperature effect (eq. 1):

$$224 \quad F_s(t_d) = \sum_{d_0}^{d_s} f(t_d) \quad eq. 1$$

225 where  $t_d$  is the daily temperature,  $f()$  is the function describing the temperature response (described  
 226 later),  $d_0$  is the first date of the developmental phase,  $d_s$  the day of the end of the developmental phase  
 227 and  $F_s(t_d)$  represents the cumulated temperatures (forcing units).

228  
 229 According to Baumgärtner et al. (2012),  $d_0$  (first date of the developmental phase) depends on the  
 230 latitude and the photoperiod. The analysis of the equations and the parameters proposed by  
 231 Baumgärtner et al. (2012) to simulate the end of diapause, allowed us to propose a simplification of  
 232 the original equations (described in ESM2) using daily values and considering a photoperiod threshold  
 233 set at 12h to stop the development of the last generation. The final proposed equations can be  
 234 described as following:

$$235 \quad F(t_d) = \sum_{d_0}^{d_s} (f(t_d) * g(P_d)) \quad or \quad F(t_d) = \sum_{d_0}^{d_s} (f(t_d) + g(P_d)) \quad eq. 2$$

$$236 \quad \text{where} \quad g(P_d) = \begin{cases} 0 & \\ \frac{P_d - P_{low}}{P_{high} - P_{low}} & P_d \leq P_{low} \\ 1 & P_{low} < P_d < P_{high} \end{cases} \quad eq. 3$$

237  
 238  
 239 where  $t_d$ ,  $f()$ ,  $d_0$ ,  $d_s$  and  $F_s(t_d)$  represent the same variables and parameters as in (eq. 1), and  $g()$  is the  
 240 function describing the photoperiod response and  $P_d$  is the daily photoperiod. The photoperiod  
 241 function is varying between a low and a high threshold ( $P_{low}$  and  $P_{high}$  respectively). We explored  
 242 two possibilities of combination of the temperature and photoperiod effect: the multiplicative (usually  
 243 used in other models as Wang and Engel (1998)) or the additive (as proposed by Baumgärtner et al.  
 244 (2012))

245 **2.2.2 Temperature response functions**

246 We tested three different functions to describe the response of *L. botrana* development to temperature  
 247 (Fig.3):

248 1) The Richardson model (R) (Richardson et al. 1974) is a step function that assumes a linear  
 249 response of development to daily temperatures for temperatures in the range Tlow to Thigh:

$$250 \quad f(t_d) = \begin{cases} 0, & t_d \leq T_{low} \\ t_d - T_{low}, & T_{low} < t_d < T_{high} \\ T_{high} - T_{low}, & t_d \geq T_{high} \end{cases} \quad eq. 4$$

251 Such approaches have been used by Arca et al. (1993) to calculate the emergence of adults and larvae  
 252 of *L. botrana*.

253 2) The Triangular model (T) (Hänninen 1990) assumes a linear, positive response to daily  
 254 temperatures for  $t_d$  in the range Tmin to Topt, and an linear but negative response for  $t_d$  in the range  
 255 Topt to Tmax (Maiorano et al. 2012):

$$256 \quad f(t_d) = \begin{cases} 0, & t_d \leq T_{min} \\ \frac{t_d - T_{min}}{T_{opt} - T_{min}}, & T_{min} < t_d \leq T_{opt} \\ \frac{t_d - T_{max}}{T_{opt} - T_{max}}, & T_{opt} < t_d < T_{max} \\ 0, & t_d \geq T_{max} \end{cases} \quad eq. 5$$

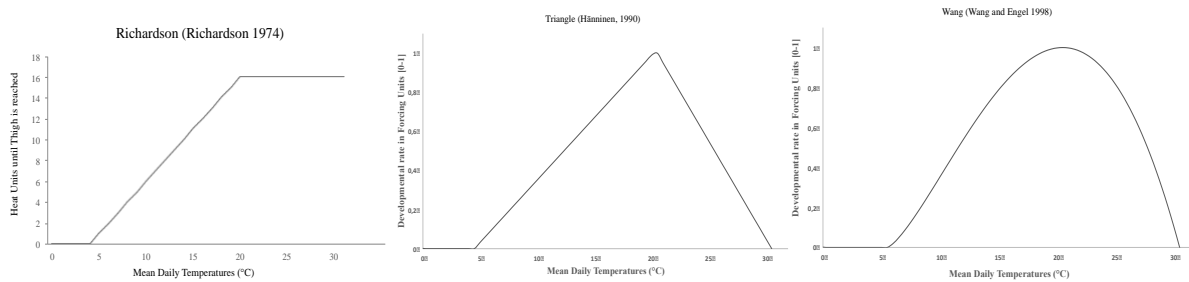
257  
 258 3) The Wang model (W) (Wang and Engel 1998) is a Beta function that considers three  
 259 cardinal temperatures Tmin, Tmax and Topt:

$$260 \quad f(t_d) = \begin{cases} 0, & t_d \leq T_{min} \\ \frac{2(t_d - T_{min})^\alpha (T_{max} - t_d)^\alpha - (t_d - T_{min})^{2\alpha}}{(T_{opt} - T_{min})^{2\alpha}}, & T_{min} < t_d < T_{max} \\ 0, & t_d \geq T_{max} \end{cases} \quad eq. 6$$

261 where

$$262 \quad \alpha = \ln(2) / \ln\left(\frac{T_{max} - T_{min}}{T_{opt} - T_{min}}\right) \quad eq. 7$$

263 This function is very similar to other functions described in the literature to simulate *L. botrana*  
 264 response to the temperature (Wang and Engel 1998) and have been applied by Milonas et al. (2001),  
 265 Briere and Pracros (1998), Logan et al. (1976) and Baumgärtner et al. (2012) for *L. botrana*.



266  
 267 **Fig. 3.** Comparison of three different approaches (Richardson, Triangle or Wang) of response to temperature  
 268 with model parameters adapted to *L. botrana*. The three representations use the same parameters with  $T_{min}=5^{\circ}C$ ,  
 269  $T_{opt}=20^{\circ}C$  and  $T_{max}=30^{\circ}C$ , except for Richardson that only uses  $T_{low}=5^{\circ}C$  and  $T_{high}=20^{\circ}C$ .

### 270 **2.2.3 Modelling parameterization and evaluation framework**

#### 271 **Overwintering submodel**

272 We assume that the overwintering starts ( $d_{i0}$ ) when day length is more than 12 hours (Roditakis and  
273 Karandinos 2001; Baumgärtner et al. 2012). Individuals that enter into prediapause in the year  $n$   
274 (autumn) will overwinter (spring) in the following year. Diapause induction starts when the day length  
275 falls below <14 hours, with a critical threshold at <12hours (Fig.2), According to this assumption and  
276 (eq.1, 2 and 3) of Baumgärtner et al. (2012), it is possible to define when the first cohort begins its  
277 diapause.

278 The diapause is a combination of temperature and photoperiod. The DOY of diapause induction was  
279 evaluated according to (eq.3) in Baumgärtner et al. (2012) calculating the day-length as a function of  
280 the DOY and the latitude. In spite of the fact that (eq.3) predicts a critical day-length threshold  
281 increasing linearly with latitude, the DOY allowing diapause induction does not vary significantly  
282 with latitude, ranging from DOY 183 to DOY 193 across our sites. For this reason, we tested the  
283 sensibility of the model to different starting date ( $d_{i0}$ ), July 1<sup>st</sup> for the southernest site and the July 15<sup>th</sup>  
284 as an average date for all the sites.

285 The post-diapause depends on temperature to allow the emergence of the first generation of adults.  
286 The cumulation of thermal accumulation from the prediapause to the post-diapause determines the  
287 first adult flights. This first sub model (overwintering) was necessary to determine the start of the  
288 calculation of the 10% of flight of the adults from the 1<sup>st</sup> generation (G1-10%).

289

#### 290 **Submodel for the adults flights**

291 In order to simulate the 10% and the 50% of each generation, we made the three following  
292 assumptions:

- 293 1. eggs laid by G1-10% (or G1-50%) adult will reach the adult stage at G2-10% (or G2-50%)  
294 and this hypothesis is valid for all the following generations ( $G_n$ -10% or  $G_n$ -50%);
- 295 2. the same functions and set of parameters can be used to simulate the thermal time  
296 accumulation between G1-10% and G2-10% (or  $G_{(n-1)}$ -10% and  $G_n$ -10%),  $G_{(n-1)}$ -50% and  
297  $G_n$ -50%, as well as  $G_n$ -10% and  $G_n$ -50%;
- 298 3. the same set of parameters can be used for all sites (and generations) without significant  
299 repercussions on the quality of the simulations (if compared to results obtained with site  
300 specific parameters) (Parker et al. 2011).

301

302 We calibrated and tested the three models Richardson (R), Triangle (T) and Wang (W) for the 10%-  
303 10% and 50%-50% of adult flights between the generations and the 10%-50% of adult flights within  
304 the generation itself. Preliminary simulations were made with all parameters, called Allp, meaning that  
305 the model calculates alone without any restriction of parameters (ESM8).

306 At the same time we also tested different sets of parameters ( $T_{min}=0^{\circ}C$ ,  $5^{\circ}C$ ,  $7^{\circ}C$ ;  $T_{max}=28^{\circ}C$ ,  
307  $33^{\circ}C$ ) Gutierrez's (2012) parameters ( $T_{min}=8.9^{\circ}C$ ,  $T_{opt}=30.8^{\circ}C$  and  $T_{max}=33^{\circ}C$ ) and some  
308 Baumgärtner's (2012) parameters ( $T_{min}=4.5^{\circ}C$ ) (ESM6, 7 and 8).

309

#### 310 **2.2.4 Calibration of the model**

311 For the purpose of calibration and testing, we split the original data into a calibration dataset (75% of  
312 the total sample selected randomly – CAL dataset) and a validation dataset (25% of the data – VAL  
313 dataset) (Picard and Cook 1984). The calibration of the parameters for the overwintering stage and the  
314 adult generations were made separately. Once the models and parameters were determined, we joined  
315 the two submodels to run the simulations with our calibration data set and validate it with the  
316 validation dataset. Finally in order to provide the best set of parameters, we recalibrated the entire  
317 model using all the database (ALL dataset) using a cross validation method (Cleland et al. 2007). The  
318 best parameters were selected according to the results of the statistical criteria described in Tab.3. The  
319 performance criteria were defined using the variance global of the observed data (STOT), the Sum of  
320 Squares Residuals (SRES), the Root Mean Square Error (RMSE), the efficiency of the model (EFF)  
321 and the Akaike test (AIC). For more details on the description and the formulas, see the ESM3 and 8.

322

#### 323 **2.2.5 Software**

324 To facilitate the development and the parameterization of this phenological model, the PMP software  
325 (Phenology Modelling Platform - PMP 5.5) has been used (downloaded from:  
326 <http://www.cefe.cnrs.fr/en/logiciels/ressources-documentaires>). PMP allows constructing, fitting and  
327 running simulations of a phenological model using meteorological data and phenological observations  
328 (Chuine et al. 2013).

329

### 330 **3. Results**

331 In this section we describe the results obtained from the calibration and the validation of both sub-  
332 models: 1) the first sub model describing the overwintering period; 2) the second sub-model which  
333 simulates the 10-10%, 50-50% and 10-50% of the different generations of adults.

334

#### 335 **3.1 Overwintering submodel**

##### 336 ***Model three phases testing R, T and W models with CAL, VAL and ALL data set***

337 As described previously we tested different versions of the submodel for the three phases of  
338 overwintering (Fig.2): 1) different functions for temperature responses (R,T,W); 2) different starting  
339 dates of prediapause ( $d_{0}$ ) (July 1<sup>st</sup> and July 15<sup>th</sup>), 3) different ways to combine temperature (T) and  
340 photoperiod (P) responses during the diapause period, using an additive (Sum) and multiplicative  
341 (Mult) factor. The best models obtained used the T and W functions, starting on 15<sup>th</sup> July ( $d_{0}$ ) and  
342 multiplying the temperature and photoperiod effects. Tab.3 describes only results obtained with CAL

343 data set with a start date ( $d_{t0}$ ) on July 15<sup>th</sup> and using a multiplicative (Mult) method for combining  
 344 photoperiod and temperature (for further results concerning all dates and methods, see ESM4). The  
 345 best results were obtained with the Triangle and Wang approaches showing EFF values of 0.77 and  
 346 0.74 respectively (Tab.3). The combination method of the functions had more impact on the results  
 347 than the starting dates named ( $d_{t0}$ ). Moreover, the date of entry in prediapa use was coherent with  
 348 Baumgärtner's values (Baumgärtner et al. 2012).

349  
 350 **Tab.3.** Performance statistics with the CAL data set for three different choices of the temperature response  
 351 function and the model version that combines temperature and photoperiod responses as multiplicative factors.  
 352 Results presented here refer to simulation with parameter values taken from the literature. The statistical analysis  
 353 use the RMSE (Root Mean Square Error) EFF (Efficiency of the model) and AIC (Akaike test).

Function	Simulations		Statistics		
	( $d_{t0}$ )	Nb data	RMSE	EFF	AIC
R	July 15th	39	9.47	0.58	98.71
T	July 15th	39	7.02	0.77	118.28
W	July 15th	39	7.49	0.74	123.22

354  
 355  
 356 **Tab.4.** Comparison of the best fitting of T (Triangle) and W (Wang) simulations to represent the overwintering  
 357 with CAL data and using a multiplicative factor. Parameters in **bold** are fixed parameters. Parameters with an \*  
 358 are from the literature (Baumgärtner, et al. 2012; Brière et al., 1999; Gutierrez et al. 2012). The other one are  
 359 free. The models 1 and 2 have free parameters. The models 3 and 4 have the parameters fixed from the models 1  
 360 and 2 and a fixed Tmin at 4.5°C as in Baumgärtner (2012) or BAUM. The models 5 and 6 consider Gutierrez's  
 361 parameters (GUT) with free day length (DL). The models 7 and 8 have fixed parameters from GUT but the DL  
 362 and Tmin for the 3rd phase of GUT are free. Gutierrez's or GUT parameters are Tmin=8.9°C, Topt=30.8°C and  
 363 Tmax=33°C.

Model		TAllp (1)	WAllp (2)	TAllp_Tmin 4.5(BAUM) (3)	WAllpT_min 4.5(BAUM) (4)	T GUT (5)	W GUT (6)	T Mult (7)	W Mult (8)
Over-wintering phases	Parameter	All free	All free	ParTAllp +Tmin= 4.5(BAUM)	ParWAllp +Tmin= 4.5 (BAUM)	GUT+Tmin= 4.5 (BAUM)+ DL Free	GUT+Tmin= 4.5 (BAUM)+ DL Free	GUT+ (Tmin & DL Free)	GUT+ (Tmin & DL Free)
	( $d_{t0}$ )	July 15th	July 15th	July 15th	July 15th	July 15th	July 15th	July 15th	July 15th
1st phase Prediapa use	Tmin	4.94	2.45	<b>4.94</b>	<b>2.45</b>	<b>8.9*</b>	<b>8.9*</b>	<b>8.9*</b>	<b>8.9*</b>
	Topt	18.76	14.36	<b>18.76</b>	<b>14.36</b>	<b>30.8*</b>	<b>30.8*</b>	<b>30.8*</b>	<b>30.8*</b>
	Tmax	28.19	27.69	<b>28.19</b>	<b>27.69</b>	<b>33*</b>	<b>33*</b>	<b>33*</b>	<b>33*</b>
2nd phase Diapause	Tmin	5.29	7.66	<b>5.29</b>	<b>7.66</b>	<b>7.1*</b>	<b>7.1*</b>	<b>7.1*</b>	<b>7.1*</b>
	Topt	16.23	15.04	<b>16.23</b>	<b>15.04</b>	<b>24.1*</b>	<b>24.1*</b>	<b>24.1*</b>	<b>24.1*</b>
	Tmax	21.89	22.87	<b>21.89</b>	<b>22.87</b>	<b>28.5*</b>	<b>28.5*</b>	<b>28.5*</b>	<b>28.5*</b>
	Plow	9.35	9.17	<b>9.35</b>	<b>9.17</b>	12.12	8.78	12.13	3.58
	Popt	13.05	14.25	<b>13.05</b>	<b>14.25</b>	16.23	13.04	16.46	7.72
3rd phase Post-diapause	Tmin	10.47	11.39	<b>4.5*</b>	<b>4.5*</b>	<b>4.5*</b>	<b>4.5*</b>	4.4	16.18
	Topt	10.48	11.42	<b>10.48</b>	<b>11.42</b>	<b>30.8*</b>	<b>30.8*</b>	<b>30.8*</b>	<b>30.8*</b>
	Tmax	20	20	<b>20</b>	<b>20</b>	<b>33*</b>	<b>33*</b>	<b>33*</b>	<b>33*</b>
Statistics	EFF	0.77	0.74	0.67	0.69	0.30	-29.81	0.30	-5.92
	AIC	118.28	123.22	161.80	158.68	185.79	329.76	183.50	270.79

364

365 To evaluate parameter sensitivity, we compare the two best models (models 1 and 2 in Tab.4), with  
 366 various models using the same functions but fixing some of their parameters from the literature  
 367 (Tab.4). Because Tmin and Topt values for the post-diapause phase were close to one another, we  
 368 explored the impact of fixing Tmin value to 4.5°C according to Baumgärtner et al.(2012) keeping all  
 369 the other parameters from the best models. Results obtained for both models (models 3 and 4 in Tab.4)  
 370 show that this parameter does not degrade the quality substantially (values of efficiency of 0.67 to  
 371 0.69).

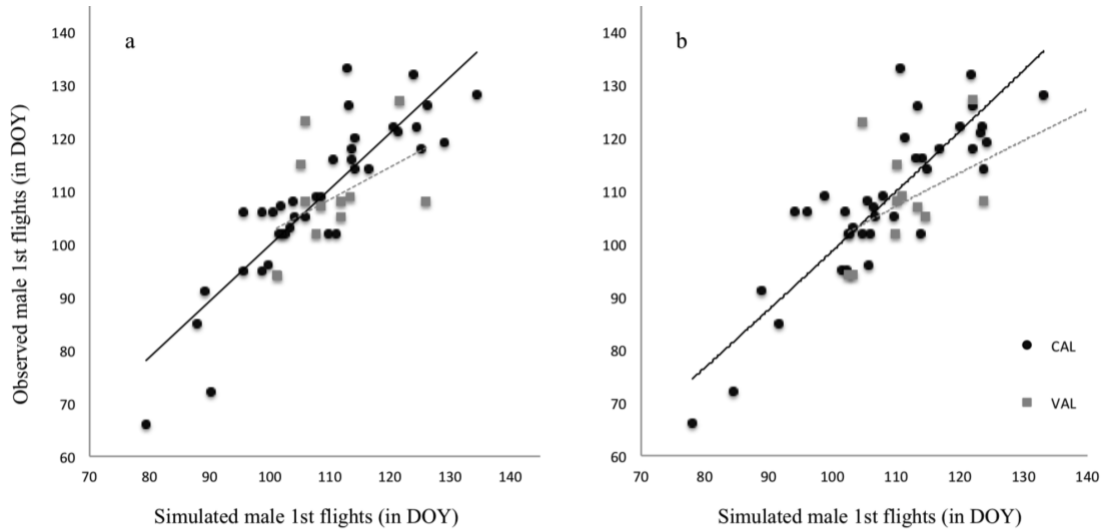
372 In order to explore other values of parameters from the literature, we tested Gutierrez et al. (2012)  
 373 parameters (GUT parameters are Tmin=8.9°C, Topt=30.8°C and Tmax=33°C) for all the temperature  
 374 thresholds with free day length (DL) and limiting the post-diapause with BAUM Tmin=4.5°C (models  
 375 5 and 6 in Tab.4), and with the Tmin free for the post-diapause phase (models 7 and 8 in Tab.4).  
 376 Results obtained show that these parameters combination decrease significantly the quality of the  
 377 model, having a higher effect when using the W function.

378  
 379 **Tab.5.** Validation of the overwintering models for both Triangle and Wang models with (d<sub>t0</sub>)=15th July. Best  
 380 fitting for Validation tests (VAL) were made with a part of the calibration (CAL) data set. The entire data set  
 381 was then tested with the ALL the data set (CAL+VAL) using cross validation. The statistical analysis use the  
 382 STOT (Total sum of the data squared) RMSE (Root Mean Square Error) and EFF (efficiency of the model)  
 383 (ESM3).  
 384  
 385

Model	Data set used	STATISTICS				
		SRES	STOT	RMSE	EFF	Nb Obs
T Allp	CAL	1874.23	8067.08	7.02	0.77	39
	VAL	969.45	1072.69	8.99	0.1	12
	ALL	3839.42	9410.59	8.68	<b>0.59</b>	51
Model	Data set used	SRES	STOT	RMSE	EFF	Nb Obs
W Allp	CAL	2134.56	8067.08	7.49	0.74	39
	VAL	1293.39	1072.69	9.07	0.08	12
	ALL	2845.7	9410.59	7.47	<b>0.7</b>	51

386  
 387 In order to provide the best set of parameters we validated the defined best models (T and W) using  
 388 the validation (VAL) data set (Tab.5). In contrast to CAL (39 data points), the validation data (VAL)  
 389 include only 12, randomly chosen observations. For this reason, apart for a low value of EFF (0.1 and  
 390 0.08) the performance statistics for VAL are more than satisfactory, with RMSE=8.99 and AIC=52.7.  
 391 After a first screening the different model configurations, we calibrated T and W using all available  
 392 data (dataset ALL). For both response functions EFF > 0.5 (0.59 for T, 0.70 for W, respectively).  
 393 Satisfactory were also the values of the RMSE (8.68 for T, and 7.47 for W, respectively) (Fig.4). We  
 394 also selected W to simulate the first flight in our model as it seems to be the more stable with all the  
 395 simulations made, with fixed or free parameterization.





**Fig.4:** Representation of the day of the first flight of *L. botrana* male with a ( $d_{t0}$ )=15<sup>th</sup> of July and a multiplicative factor: a) Triangle model b) Wang model. Simulated and observed data in DOY (Julian days) show the quality of the simulation for each data set where CAL are in black circle and the results from the validation model VAL are in grey squares.

### 3.2 Submodel for the adults flights

We again tested different temperature response functions (R, W, T) to evaluate their performance to simulate adult flights between two consecutive generations (10-10%; 50-50%) and within a generation itself (10-50%). Following the same methodology as for the first flight, simulations were carried out by specifying all the parameters as free parameters (to be calibrated) or fixing some of them at values obtained from the literature. Summary statistics are presented in Tab.6.

#### 3.2.1 Simulation the 10-10%-50-50% between the generations

According to the first assumption described in the modelling framework (see Material and Methods section), we explore the capacity of the model to represent with a single set of parameters all the 10-10% and 50%-50% generations.

**Tab.6.** Simulation of the model hypothesis testing the 10-10%/50-50% between the *L. botrana* generations with the calibration (CAL) and validation (VAL) data set. The statistical analysis use the RMSE (Root Mean Square Error) and EFF (efficiency of the model). GUT parameters are  $T_{min}=8.9^{\circ}C$ ,  $T_{opt}=30.8^{\circ}C$  and  $T_{max}=33^{\circ}C$ .

10-10%-50-50% between generations				Statistics	
	Simulation	Data set	Nb data	RMSE	EFF
R Allp	10-10 / 50-50	CAL	140	6.97	0.95
R ParGUT		CAL	140	8.35	0.93
R ParAllp (VAL)		VAL	46	11.00	0.84
	Simulation	Data set	Nb data	RMSE	EFF
T Allp	10-10 / 50-50	CAL	140	6.93	0.95
T ParGUT		CAL	140	8.32	0.93
T ParAllp (VAL)		VAL	46	11.08	0.84
	Simulation	Data set	Nb data	RMSE	EFF
W Allp	10-10 / 50-50	CAL	140	6.93	0.95
W ParGUT		CAL	140	27.96	0.25
W ParAllp (VAL)		VAL	46	11.15	0.84

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The three models in Tab.6 had high values of EFF when all the parameters are fitted (around 0.95). Values of the EFF decreased when some of the parameters were fixed (values varying between 0.25 to 0.95 depending on the model). We also validated the best model (Allp model) with the independent VAL dataset and we obtained good efficiency values for all the models (EFF = 0.84). As for the overwintering model, we propose to exclude R from our analysis because its structure to describe the development of *L. botrana* does not integrate maximum temperature (Tmax) even if the calibration did not show a significant effect of this threshold. Moreover, as in the overwintering model, the test using Gutierrez's parameters did not improve the simulation even if we obtained better results than with the overwintering models. Finally, the W function with Tmin=2.4°C, Topt=23.12°C and Tmax=32.13°C was the best one with free parameters (see ESM7) and the closer to the known biological behaviour of *L. botrana* according to the literature.

Indeed, we also explored the sensitivity of each group (10-10% and 50-50%) separately and comparing the values of these parameters to the previously obtained. This analysis allowed evaluating their robustness to simulate each phase independently (Tab.7).

**Tab.7.** Crossed models separating the 10-10% and 50-50% between generations of *L. botrana* with CAL data set. Tests are made with free parameters and with the parameters of the best simulation from CAL Allp, testing the 10-10% /50-50% between generation. The statistical analysis use the RMSE and EFF. Gutierrez's or GUT parameters are Tmin=8.9°C, Topt=30.8°C and Tmax=33°C.

10-10%-50-50% between generations			Statistics	
R 10-10%	Simulation	Nb data	RMSE	EFF
R Allp			8.12	0.93
R ParCal Allp	10 - 10	93	8.26	0.93
R ParGUT			8.81	0.92
<b>R 50-50%</b>			<b>RMSE</b>	<b>EFF</b>
R Allp		<b>Nb data</b>	7.77	0.94
R ParCal Allp	50-50	93	7.87	0.94
R ParGUT			9.06	0.92
<b>T 10-10%</b>			<b>RMSE</b>	<b>EFF</b>
T Allp (10-10%)		<b>Nb data</b>	8.17	0.93
T ParCal Allp	10 - 10	93	8.31	0.93
T ParGUT			8.79	0.92
<b>T 50-50%</b>			<b>RMSE</b>	<b>EFF</b>
T Allp (50-50%)		<b>Nb data</b>	7.72	0.94
T ParCal Allp	50-50	93	7.81	0.94
T ParGUT			9.03	0.92
<b>W 10-10%</b>			<b>RMSE</b>	<b>EFF</b>
W Allp (10-10%)		<b>Nb data</b>	8.11	0.93
W ParCal Allp	10 - 10	93	8.33	0.92
W ParGUT			26.14	0.26
<b>W 50-50%</b>			<b>RMSE</b>	<b>EFF</b>
W Allp		<b>Nb data</b>	7.74	0.94
W ParCal Allp	50-50	93	7.86	0.94
W ParGUT			27.77	0.21

439 Results obtained in Tab.7 show that the models simulate correctly the 10-10% and the 50-50%  
 440 generations when we consider parameters from the first calibration (Tab.6) and with all parameters

441 free but separating 10 – 10% and 50 – 50% in different datasets (for parameters values see in ESM3).  
 442 The EFF was around 0.92 and 0.94 and the RMSE between 7 and 8 days for the three functions (R, T  
 443 and W). Indeed, when using Gutierrez’s parameters, the R and T models showed good results  
 444 (EFF=0.92), which was not the case for the W model that degraded (EFF=0.21 and 0.26). This  
 445 analysis confirms the robustness of the model and its parameters, allowing to use a single function to  
 446 simulate all the generations of one cycle for the 10 to 10% and 50 to 50% values for each generation.

447

### 448 3.2.2 Simulation 10%-50% of adults flights within a generation itself

449 As previously reported (Fig.2) results presented in the following refer to simulations with no  
 450 difference in parameter values between different generations.

451

452 **Tab.8:** Simulation of the 10-50% of *L. botrana* adults flights within a generation itself with CAL, VAL and  
 453 ALL data set. The statistical analysis use the RMSE (Root Mean Square Error) and EFF (model efficiency).  
 454 Gutierrez’s or GUT parameters are Tmin=8.9°C, Topt=30.8°C and Tmax=33°C.

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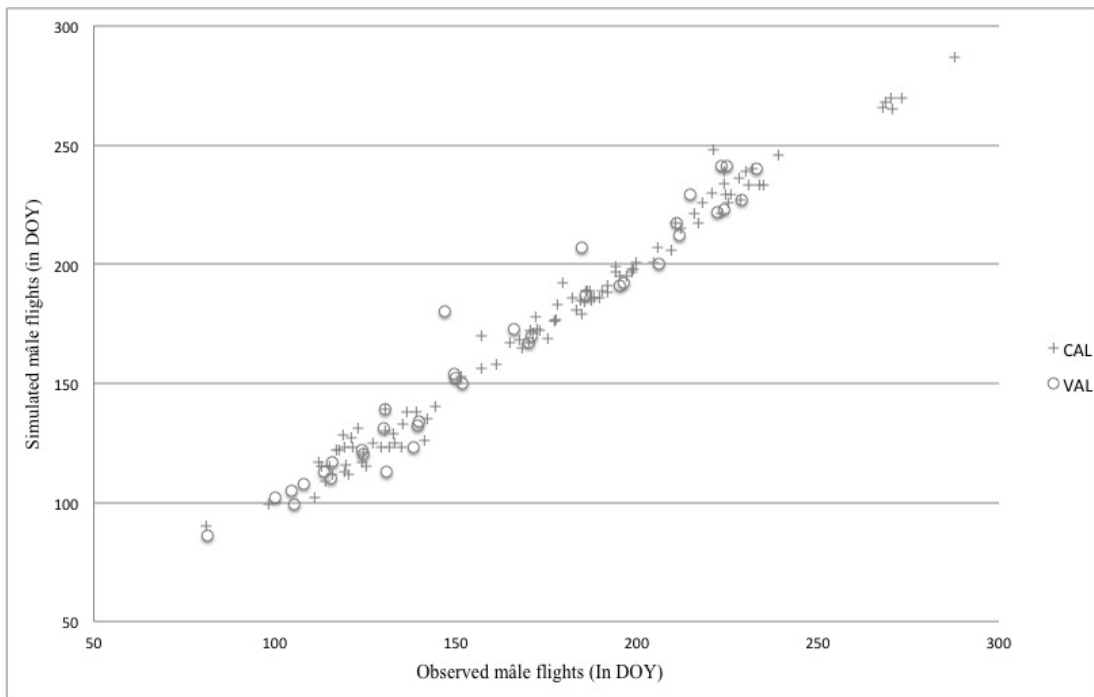
10%-50% within a generation itself			Statistics	
Model R 10-50%	Nb data	Data set	RMSE	EFF
R CAL Allp			5.59	0.99
R CAL ParCAL_Allp10-10	107	CAL	5.93	0.98
R ParGUT			6.24	0.98
R VAL Allp	37	VAL	10.93	0.95
R ALL	144	ALL	8.56	0.97
Model T 10-50%	Nb data	Data set	RMSE	EFF
T CAL Allp			5.53	0.99
T CAL ParCAL_Allp10-10	107	CAL	5.91	0.98
T ParGUT			6.24	0.98
T VAL Allp	37	VAL	10.02	0.96
T ALL	144	ALL	7.33	0.98
Model W 10-50%	Nb data	Data set	RMSE	EFF
W CAL Allp			5.55	0.99
W CAL ParCAL_Allp10-10	107	CAL	5.94	0.98
W ParGUT			48.04	-0.05
W VAL Allp	37	VAL	9.84	0.96
W ALL	144	ALL	7.15	0.98

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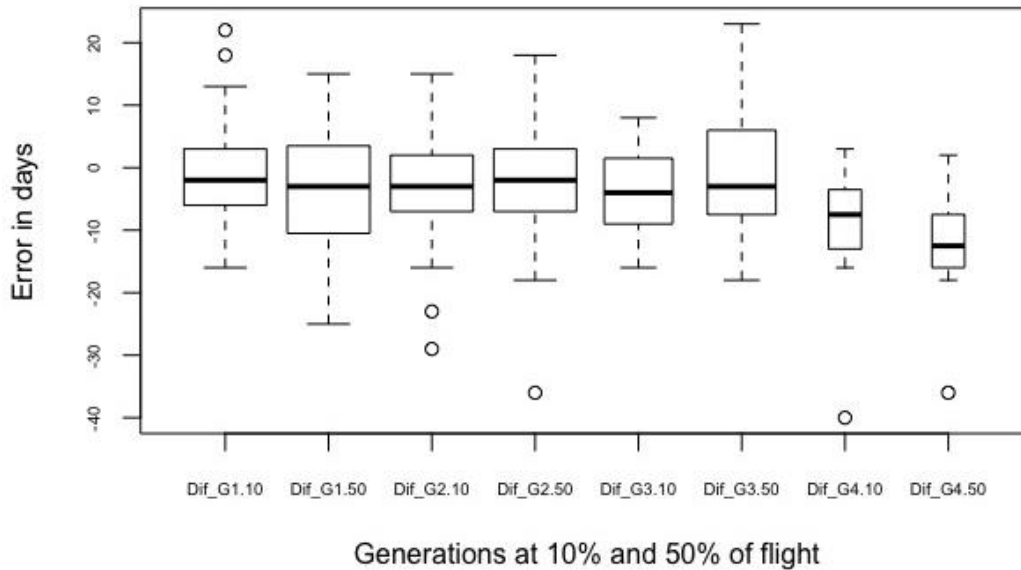
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458 Results described in Tab.8 show that very high values of EFF (from 0.98 to 0.99) were obtained  
 459 irrespective of the model configuration. Fixing parameters for the W model to the values suggested by  
 460 Gutierrez et al. (2012) significantly degraded the results (EFF = -0.05). In line with the previous tests,  
 461 the sensitivity of these models have been tested fixing some parameters (Tlow/Tmin and Tmax in  
 462 ESM5 and 6). All the parameters found are close to the ones known in the literature so we kept them  
 463 fixed (Tmin=8.9°C, Topt=30.8°C and Tmax=33°C in GUT or Tmin=4.5°C in Baumgärtner et al.,  
 464 (2012)). In the first simulations with CAL data set and using free parameters (All parameters free), W  
 465 seems to achieve better performances than T and R. Indeed, with fixed parameters the results did not  
 466 improve with an RMSE around 5.5 days for the 3 functions and with parameters whose values are  
 467 close to those found in the literature. We also validated the best model (All parameters free model)

468 with the independent VAL dataset and we obtained good efficiency values for all the models  
469 (EFF=0.96) and an error of 9.84 days (RMSE). Fig.5 illustrates the distribution of the simulated and  
470 observed data for the 10-50% of male flights within the same generation for the Wang model. The  
471 figure shows the good capacity of the model to simulate this phase. In general Fig.6, the box size is  
472 proportional to the number of data and shows that the error for the simulation of all the generations for  
473 all the transect study have a small error (mean of +/- 5 days) between simulated and observed data.  
474



475  
476 **Fig. 5.** Distribution of the simulated and observed data for the 10-50% of *L. botrana* male flights within the  
477 same generation with the Wang model. Simulated and observed data show here the correlation with both the  
478 results from the calibration model (CAL with crosses) and the results from the validation model (VAL with  
479 circles).  
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**Fig. 6.** Error between observation and simulations in number of days of the 10% and 50% of each generation of *L. botrana* flights, all site and years confounded. The errors fluctuate around 10 days before or after the observation data in the boxplots, with some extreme data, also present in the observed data. The last generations (G4.10 and G4.50) show a larger difference between observation and predictions, probably due to the sparsity of data that we disposed of, as only 2 sites had a 4<sup>th</sup> generation. The size of the boxes is proportional to the number of data.

#### 489 4. General discussion of the results

490 This study examined the possibility to assemble a simple, robust, generic, yet process-based model for  
491 simulating the voltinism of *L. botrana*. This model can be useful for large scale studies and impact  
492 studies targeting the behaviour of the insect pests under future climate change. The analysis of existing  
493 model indicated that two phases (overwintering and adults) are necessary to realistically represent the  
494 life cycle of *L. botrana*. The methodology to calculate the voltinism was based on the 10% and 50% of  
495 the total male flights per generation as significant reference to make simulations.

496 Data used for model development and testing were obtained from a wide latitudinal transect, allowing  
497 to test the possibility to apply the model at large scales.

498 The parameterization of the model was made by analysing different published models (Tab.1). Three  
499 types of temperature response functions were examined: Richardson, Triangle and Wang. The  
500 evaluation results showed that T and W are very close in their performance. The analysis provided  
501 good results with or without the use of certain specific parameter values found in the literature.  
502 Moreover, the sensitivity of the models to different sets of parameters from the literature used by  
503 Baumgärtner et al. (2012) and Gutierrez et al. (2012) did not improved the results of the  
504 parameterization tests with free parameters (Allp). On the contrary, the tests made with the Gutierrez's  
505 parameters degraded the results (Tab.8).

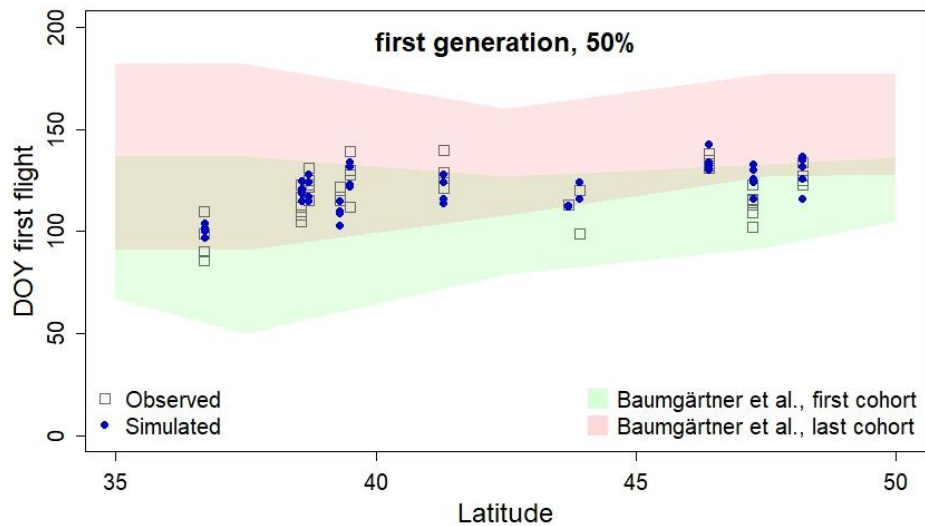
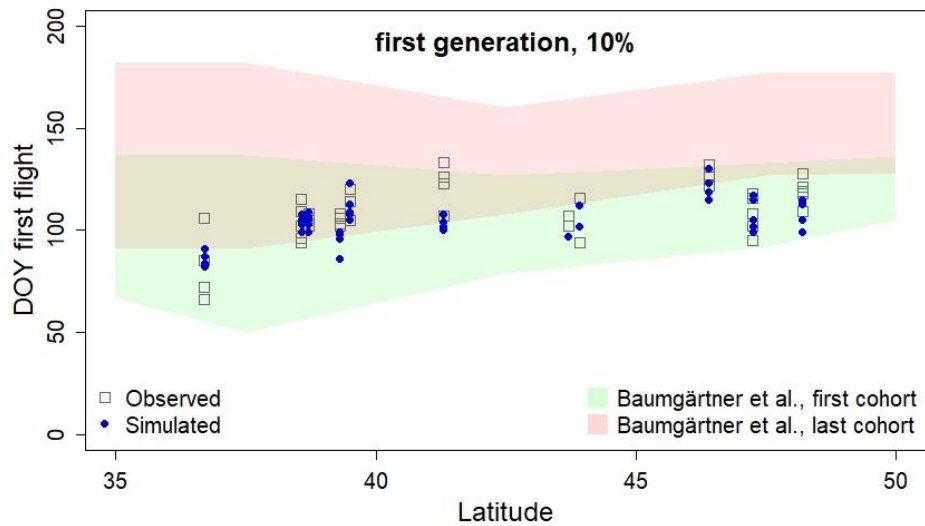
506 Another issue raised in our study was to integrate the photoperiod in a large latitudinal transect (from  
507 Lat.36.710°N to Lat.48.213°N) and understand its interaction with temperatures (as multiplicative or  
508 additive factor). The analysis of this interaction (Tab.3 and 4) showed that the multiplicative approach  
509 was better adapted to describe these interactions than the additive approach proposed by Baumgärtner  
510 et al. (2012) (ESM2). In any case, the multiplicative approach is the one commonly implemented in  
511 complex models and usually performs accurately (Briere and Pracros 1998; Wang and Engel 1998;  
512 Baumgärtner et al. 2012). Finally, the analysis also indicated that assuming a common diapause  
513 starting date, ( $d_{i0}$ ) = July 15<sup>th</sup>, for the entire transect was a reasonable choice.

514 We show that LGM is able to correctly represent the life cycle of *L. botrana* in various areas with the  
515 same set of parameters, with a model performance comparable to the one of local models (Parker et al.  
516 2011). This model is based on existing models but applied at other scale and consider less parameters  
517 that make its use easier. This approach is different to the previous one as it can be applied for large  
518 scale studies like climate change scenarios.

#### 519 **4.1 Proposal for a new model**

520 The LGM uses a simplification of Baumgärtner's approach only to calculate the first cohort and not  
521 the entire population of *L. botrana* as in the original function. The overwintering submodel considers  
522 the general approach of the sum of temperatures (i.e. cumulation of temperatures as GDD or Growing  
523 Degree Days) and not the speed of growing as in Baumgärtner's original function. Then, the adults  
524 submodel uses the same parameters to cumulate heat between and within the generations. As we  
525 describe in the Fig.7, the LGM model and Baumgärtner's model have the same range of errors to  
526 simulate the first cohort of a *L. botrana* population even with a simplification of the calculation  
527 methods. This comparison between both models provided a second partial validation of the LGM  
528 model, because it is not exhaustive as the years (observations) and sites (latitude) are different in both  
529 studies.

530



531

532 **Fig.7:** Comparison between LGM observed and simulated adults flights of *L. botrana* in DOY (Day of Year) and  
 533 Baumgärtner's first and last cohort observations. From a geographical perspective, both models consider a wide  
 534 range of sites and climates. The simulations of G1-10% and observations both fall within the spread of the first  
 535 cohort appearing (in green) in Baumgärtner's model. The same observations can be made with the G1-50% that  
 536 fall within the spread of the last cohort appearing (in red) in Baumgärtner's model.

537

538 In the LGM, the results of the different tests showed similar performances for all models and  
 539 developmental phases studied. We nevertheless propose to use the W model to simulate different  
 540 temperature responses because it better reflects the known biological response of *L. botrana* to  
 541 temperature. Thus, Wang is the unique function used to simulate both overwintering (Predia, dia and  
 542 Post-dia) and adult flights submodels. This is a classical approach using a first model with the  
 543 calibration and validation data sets. A preliminary analysis revealed that the small divergence between  
 544 the models allowed us to test another model with all the data sets. Tab.9 provides the statistical  
 545 analysis with all the parameter values used for the calibration, validation and the entire data set.

546 It summarizes the proposed model, LGM model, showing the different parameter sets used to simulate  
 547 the three phases of the overwintering period, but the single, common set of parameters used to  
 548 simulate all the phases (10% and 50%) of the different generations of the adults flights.

549  
 550 **Tab.9.** Final submodels selected for their efficiency according to the calibration (CAL), validation (VAL) and  
 551 the full data set (ALL) of samples and the stability of their biological response to temperature. Both set of  
 552 parameters obtained using the 10% and 50% between the generations of the *L. botrana* adults flights and the 10-  
 553 10%/50-50% within the generations are presented. The final results for the Wang model are close to biological  
 554 thresholds reported in the literature, particularly those published by Gutierrez et al. (2012).

Models	Parameters							Statistics					
	Phases	Tmin	Topt	Tmax	Plow	Phigh	F	CAL			VAL		
								RMSE	EFF	Nb Obs	RMSE	EFF	Nb Obs
WAllp	Predia	2,45	14,36	27,69	-	-	40,74						
	Dia	7,66	15,04	22,87	9,17	14,25	28,35	7,49	0,74	39	9,07	0,08	12
	Post-dia	11,39	11,42	20,00	-	-	1,47						
W ParAllp Tmin=4.5°C (BAUM)	Predia	<b>2,45</b>	<b>14,36</b>	<b>27,69</b>	-	-	<b>39,79</b>						
	Dia	<b>7,66</b>	<b>15,04</b>	<b>22,87</b>	<b>9,17</b>	<b>14,25</b>	<b>30,23</b>	8,04	0,69	39	9,04	0,09	12
	Post-dia	<b>4,50</b>	<b>11,42</b>	<b>20,00</b>	-	-	<b>2,026</b>						
W Allp 10- 10/50-50 Between g.	Adult flight	2,38	23,13	32,31	-	-	45,61	6,93	0,95	140	11,15	0,84	46
W Allp 10- 50 within g.	Adult flight	2,38	23,13	32,31	-	-	7,76	5,94	0,98	107	9,84	0,96	37

556  
 557 Concerning the adult development stage, the results confirm our hypothesis that a standard set of  
 558 parameters is sufficient to accurately simulate the voltinism of *L. botrana* from diapause to last flight  
 559 in terms of the 10% and 50% of the male flights.

560  
 561 This finding is important because, as we described in the introduction, it is common practice to  
 562 recalibrate phenological models for each generation (Beddow et al. 2010). Thus, in previous studies  
 563 (Tab.1) authors proposed a different set of parameters or models for each generation considering that  
 564 the biological response was different during the entire cycle. We are convinced that our approach  
 565 introduces more robustness into the simulation of the life cycle of *L. botrana*. Indeed, it allows  
 566 applications at large geographical scales without adapting the model to local parameters. Whether this  
 567 can also be extended to other species remains to be investigated.

#### 568 **4.2 Advantages and limits of the generic model**

569 To define the LGM, we considered the models with the best statistical criteria and the most  
 570 representative biological processes known from the literature (ESM7). One of the major difficulties  
 571 we encountered was to model the overwintering phase, as we did not dispose of data to represent the



572 associated intermediate phases (i.e., end of prediapause and end of diapause). The calibration of this  
573 complex submodel was hence performed targeting the date of the 10% of the first generation at each  
574 site. The lack of intermediate information is a common problem faced in developing phenology  
575 models for plants (Chuine et al. 2016). In our case, the data collection have been a long process and  
576 the quality selection of the male flights had to correspond to sites where we had meteorological data  
577 available close by (at least 15 years). Some authors like Amo-Salas et al. (2011) and Armendáriz et al.  
578 (2009) integrated relative humidity in their model, but they concluded that the value error with or  
579 without this parameter was not a significant influencing factor. Indeed, we did not consider relative  
580 humidity as in Baumgärtner et al. (2012), as we did not have such data available for all our sites.

581 Another limit of this study concerns the data that have been selected and converted to a comparable  
582 and standardized unit, but the observed data do not consider a protocol and the heterogeneity of the  
583 observed data can alter the quality of the calibration. Observation values obtained in the laboratory (in  
584 controlled conditions, at constant temperature), where rates of development are estimated  
585 approximately (Briere and Pracros 1999; Torres-Vila et al. 1999; Picart 2009) can differ considerably  
586 from those observed in the field and between the sites or by calibrating models using local conditions  
587 (Arca et al. 1993; Torres-Vila et al. 1999; Severini et al. 2005; Moravie et al. 2006). The large  
588 latitudinal range of study is complex, as seen in Fig.5, where some extreme values, representing the 4<sup>th</sup>  
589 generations in south of Spain (not present at other sites), fall for the CAL dataset and not in the VAL  
590 dataset due to the randomization of the data selection and can alter the EFF of the tests. Nevertheless,  
591 the strength of this study has been to obtain a stable and robust model at a large spatial scale.

592 We believe that this work has contributed to raise new questions on scale applications for applied  
593 studies like climate change and on the methodologies used to simulate insect developmental processes.  
594 The approach developed here, making use of a simple and unique set of parameters, representative of  
595 the biological response to temperatures, has shown very interesting and encouraging results.

### 596 **4.3 Future model applications**

597 We anticipate that LGM, as a model, is appropriate to conduct impact studies that integrate climate  
598 change scenarios in order to predict the future geographical distribution of ectothermic insects and the  
599 future extent of vulnerable areas. Multivoltine species are likely to develop more generations under  
600 warmer conditions (Caffarra et al. 2012; Reineke and Thiery 2016). Sensitivity analyses with LGM,  
601 combined with phenological models for plants, as grapevine for example, will allow to identify critical  
602 shifts in the synchrony or asynchrony of different trophic levels (host plants and insect pests) and the  
603 ensuing overlap periods (Hoover and Newman 2004; Hirschi et al. 2012; Stoeckli et al. 2012; Gilioli  
604 et al. 2016). Nevertheless, more data would have been useful to validate the choice of the best models.  
605 This study could be improved by testing other regions of the world or by implementing the entire set

606 of data used.

607 In concert with phenological models for crops, LGM will help raise the awareness of producers on the  
608 emergence of new threats and adaptation of future treatment practices according to geographic areas.  
609 Again, the advantages of LGM are its conceptual simplicity and generic parameterization, which allow  
610 the implementation of climate change studies at the large scale for both plants and insect pests.

611

#### 612 **Author Contribution Statement**

613 VC and IGCA conceived and designed the research and analyzed the data. PC and JM contributed new  
614 reagents and analytical tools. MB reviewed and corrected the manuscript. All authors read and  
615 approved the manuscript.

616

#### 617 **Compliance with Ethical Standards:**

618 All authors declare that they have no conflict of interest. This article does not contain any studies with  
619 animals or human participants performed by any of the authors.

620

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