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

V. Castex[a,*], I. García de Cortázar-Atauri[b], P. Calanca[c], M. Beniston[a], J. Moreau[d]

[a] Institute of Environmental Sciences, University of Geneva, Switzerland
[b] INRA, US1116 AgroClim, 84914 Avignon, France
[c] Agroscope, Agroecology and Environment, Switzerland
[d] Université de Bourgogne Franche-Comté, UMR 6282 Biogéosciences, Equipe Ecologie-Evolutive, France

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ABSTRACT

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

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

1. Introduction

Modern agriculture relies on the massive use of pesticides to increase productivity (Tilman et al., 2002). This has caused considerable stress on biodiversity and made insect pests more resistant to pesticides (Hatt et al., 2018). Furthermore, extensive commercial trade as well as increasing temperatures have enhanced the spread of insect pests. As a result, invasive species have started to damage crops in remote areas (Bale et al., 2002; Lin, 2011; Lamichhane et al., 2015). Understanding and predicting insect pest dynamics is necessary in order to ensure productivity while reducing the use of chemicals (Bregaglio et al., 2013). In the context of global warming, there is also a need to understand how pest species dynamics will evolve in the future. In this context, phenological models are interesting tools to monitor populations dynamics and to predict their evolution, e.g., under changing environmental and climatic conditions (Steinbauer et al., 2004; Nietschke et al., 2007; Stoeckli et al., 2012). Such models are capable of anticipating insects' voltinism and allows improving treatment periods (Moravie et al., 2006).

Process-based models aim to represent biological processes through equations that describe developmental, survival, fecundity or mortality rates for different life-stages of insects (from prediapause to overwintering). Among the different processes simulated, phenology (development) is probably one of the most important, because it defines the biological cycle (Chuine et al., 2013). Insects are ectotherms and consequently their physiological development is mainly driven by temperature (Zhou et al., 1995; Bale et al., 2002; Tobin et al., 2008). They exhibit a response to thermal variation (Singer and Parmesan, 2010; Bale and Hayward, 2010; Brodeur et al., 2013; Moiroux et al., 2014) by adjusting life history traits like the date of overwintering and population growth (Hance et al., 2007; Moreau et al., 2017). Diapause and overwintering are further determined by photoperiod (Pavan et al.,

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* Corresponding author at: University of Geneva – ISE, Boulevard Carl-Vogt 66, 1205 Geneva, Switzerland.
E-mail addresses: victorine.castex@unige.ch (V. Castex), inaki.garciadecortazar@inra.fr (I. García de Cortázar-Atauri), pierluigi.calanca@agroscope.admin.ch (P. Calanca), Martin.Beniston@unige.ch (M. Beniston), Jerome.Moreau@u-bourgogne.fr (J. Moreau).

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2006; Svobodová et al., 2014). Both temperature and photoperiod thus explain how insects' life cycle respond to local climatic conditions, latitude and altitude (Honěk, 1996; Ioriatti et al., 2011). Changes in the growing rate and geographical distribution of pests have already been observed in the last decades (Baumgärtner et al., 2012) as a consequence of recent changes in climate.

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

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

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

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

The overall purpose of this work is to present a generic model for *L.*

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

	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) - 1st (8; 13), 2nd (6) and 3rd (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 ($DL < 14.15$ h) (5) - Day of overwintering (previous year) (7) - Day of the 1st individual to enter in diapause (12) - End previous generation (chrysalides) (3)	- (d_{t0}) = −183 (July 15th) corresponding to the day with $>$ 12 h 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	- Population / Rate sum model (6; 9; 12) - Empirical / Biologically Based model (1; 3; 4; 6; 10; 11; 13) - Physiologically Based Demographic Model (5; 14) - Aged structure (7)	- Voltinism Process Based Model with a statistical approach
Strength	- Perform well under same conditions as considered during model development - Easy to implement if local data are available - Suitable for integration into Decision Support Tools	- 1 set of parameters - Suitable for large scale impact studies as climate change scenarios
Weakness	- Not necessarily reproducible at other sites with the same parameters (applicability to new situations needs to be verified) - Different sets of parameters for each region, generation and between the phases (based on the analysis of the different models, ESM7). - Local models are not applicable to large scale studies	- Predictions across sites are robust even if performance quality can be low in specific cases

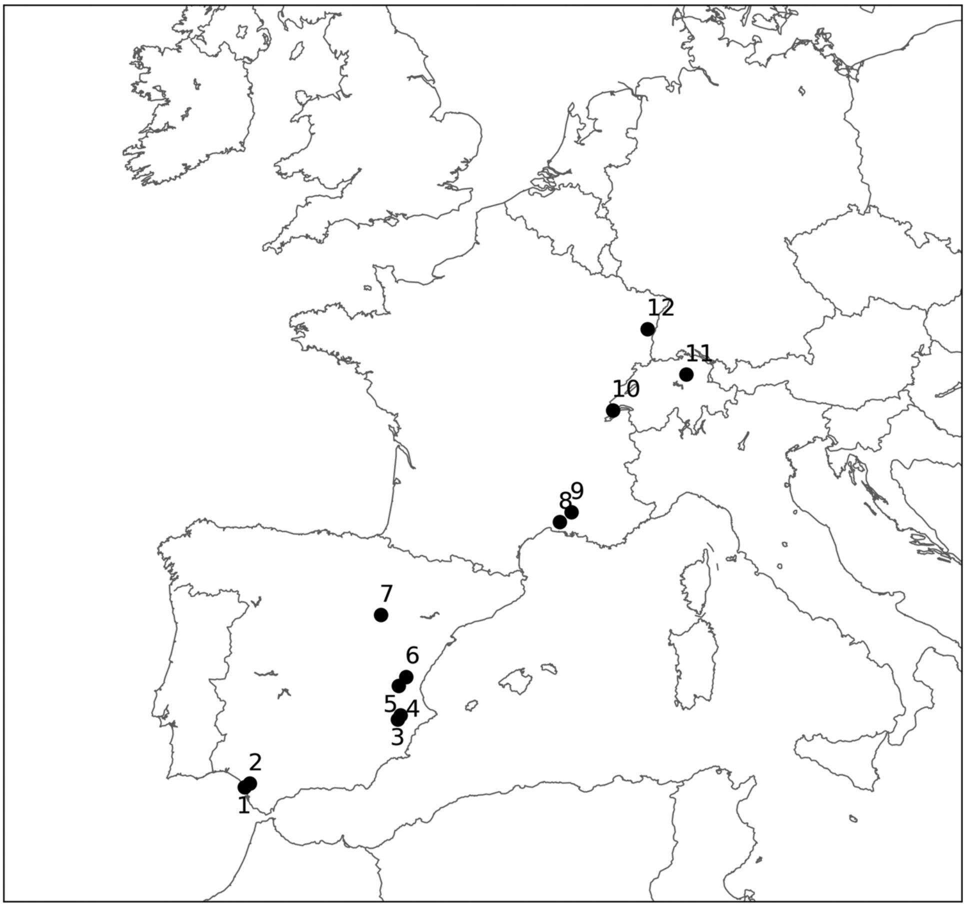


Fig. 1. Map of the study sites in Europe (produced with MakeMap from an open source code). The numbers in the map represent the study sites introduced in Table 2.

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

The specific aims of this study are 1) to analyze existing models of *L. botrana* voltinism in order to propose a generic approach for simulating representative phase of development (10 % and 50 % of the male flights) of an adult population from diapause to last flight; and 2) to propose a validated standard set of parameters for applications at the large scale. We use for this purpose a large database of flight observations compiled in a wide latitudinal transect running from southern Spain to northern France (Fig. 1) and representing Mediterranean and Continental climate types (Jongman et al., 2006; Beck et al., 2018).

2. Materials and methods

2.1. Data used in the study

2.1.1. Phenological data of L. botrana

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

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

2.1.2. Meteorological data

Meteorological data were obtained from different meteorological services at each site (Table 2). Daily minimum, maximum and mean

Table 2
L. botrana adult flights data and meteorological data acquisition per site in latitudinal order.

	Lobesia Botrana		Meteorological station				
Site Number	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

temperatures were collected from meteorological stations in an array with a maximum distance of 10 − 15 km from the collection sites of *L. botrana* flights, and almost at the same altitude as the vineyards, which we considered reasonable for the representation of local meteorological conditions.

2.2. A generic phenological model for L. botrana

2.2.1. General description of the model

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

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

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

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

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

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

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

$$\boldsymbol{F_s(t_d)} = \sum_{\boldsymbol{d_0}}^{\boldsymbol{ds}} \boldsymbol{f(t_d)} \tag{1}$$

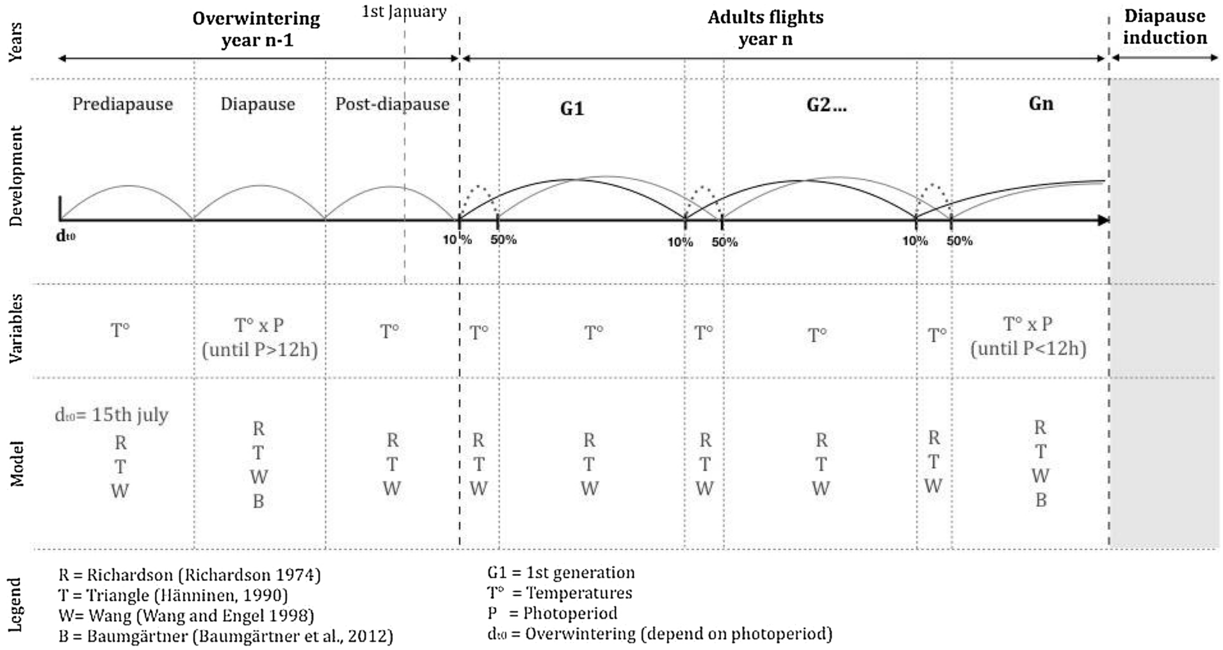
where t_d is the daily temperature, *f()* is the function describing the temperature response (described later), d_0 is the first date of the developmental phase, d_s the day of the end of the developmental phase and $F_s(t_d)$ represents the cumulated temperatures (forcing units).

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

$$\boldsymbol{F(t_d)} = \sum_{\boldsymbol{d_0}}^{\boldsymbol{d_s}} (\boldsymbol{f(t_d)}{}^*\boldsymbol{g(P_d)})\ \textbf{or}\ \boldsymbol{F(t_d)} = \sum_{\boldsymbol{d_0}}^{\boldsymbol{d_s}} (\boldsymbol{f(t_d)} + \boldsymbol{g(P_d)}) \tag{2}$$

$$\text{where}\ \boldsymbol{g(Pt_d)} = \begin{cases} 0 & \\ \dfrac{\boldsymbol{P_d - Plow}}{\boldsymbol{Phigh - Plow}} & \boldsymbol{P_d \le Plow} \\ & \boldsymbol{Plow} < \boldsymbol{P_d} < Phigh \\ 1 & \end{cases} \tag{3}$$

where t_d, *f()*, d_0, d_s and $F_s(t_d)$ represent the same variables and



Inspired from : Baumgärtner et al., 2012; Gallardo et al., 2008; Gutierrez et al., 2012 and Hänninen, 1990

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

parameters as in (Eq. (1)), and *g()* is the function describing the photoperiod response and P_d is the daily photoperiod. The photoperiod function is varying between a low and a high threshold (*Plow* and *Phigh* respectively). We explored two possibilities of combination of the temperature and photoperiod effect: the multiplicative (usually used in other models as Wang and Engel (1998) or the additive (as proposed by Baumgärtner et al. (2012))

2.2.2. Temperature response functions

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

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

$$f(t_d) = \begin{cases} 0, & \boldsymbol{t_d \le Tlow} \\ t_d - Tlow, & \boldsymbol{Tlow} < \boldsymbol{t_d} < Thigh \\ Thigh - Tlow, & \boldsymbol{t_d \ge Thigh} \end{cases} \tag{4}$$

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

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

$$f(t_d) = \begin{cases} 0, & \boldsymbol{t_d \le Tmin} \\ \dfrac{\boldsymbol{t_d - Tmin}}{\boldsymbol{Topt - Tmin}}, & \boldsymbol{Tmin} < \boldsymbol{t_d \le Topt} \\ \dfrac{\boldsymbol{t_d - Tmax}}{\boldsymbol{Topt - Tmax}}, & \boldsymbol{Topt} < \boldsymbol{t_d} < Tmax \\ 0, & \boldsymbol{t_d \ge Tmax} \end{cases} \tag{5}$$

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

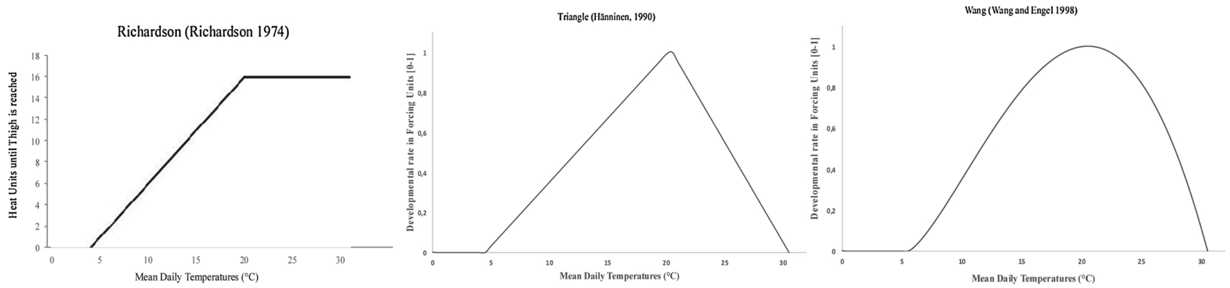


Fig. 3. Comparison of three different approaches (Richardson, Triangle or Wang) of response to temperature with model parameters adapted to *L. botrana.* The three representations use the same parameters with T_{min} = 5 °C, T_{opt} = 20 °C and T_{max} = 30 °C, except for Richardson that only uses T_{low}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

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

Simulations				Statistics	
Function	(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

$$\boldsymbol{f}(\boldsymbol{t_d}) = \begin{cases} 0, & \boldsymbol{t_d} \leq \boldsymbol{Tmin} \\ \dfrac{2(\boldsymbol{t_d} - \boldsymbol{Tmin})^{\propto}(\boldsymbol{t_d} - \boldsymbol{Tmin})^{\propto} - (\boldsymbol{t_d} - \boldsymbol{Tmin})^{2\propto}}{(\boldsymbol{Topt} - \boldsymbol{Tmin})^{2\propto}}, & \boldsymbol{Tmin} < \boldsymbol{t_d} < Tmax \\ 0, & \boldsymbol{t_d} \geq \boldsymbol{Tmax} \end{cases} \tag{6}$$

where

$$\propto = \mathbf{ln}(2)/\mathbf{ln}\left(\frac{\boldsymbol{Tmax} - \boldsymbol{Tmin}}{\boldsymbol{Topt} - \boldsymbol{Tmin}}\right) \tag{7}$$

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

2.2.3. Modelling parameterization and evaluation framework

2.2.3.1. Overwintering submodel. We assume that the overwintering starts (d_{t0}) when day length is more than 12 h (Roditakis and Karandinos, 2001; Baumgärtner et al., 2012). Individuals that enter into prediapause in the year n (autumn) will overwinter (spring) in the following year. Diapause induction starts when the day length falls below < 14 h, with a critical threshold at < 12 h (Fig. 2), According to this assumption and (Eqs. (1)–(3) of Baumgärtner et al. (2012), it is possible to define when the first cohort begins its diapause.

The diapause is a combination of temperature and photoperiod. The DOY of diapause induction was evaluated according to (Eq. (3)) in Baumgärtner et al. (2012) calculating the day-length as a function of the DOY and the latitude. In spite of the fact that (Eq. (3)) predicts a critical day-length threshold increasing linearly with latitude, the DOY allowing diapause induction does not vary significantly with latitude, ranging from DOY 183 to DOY 193 across our sites. For this reason, we tested the sensibility of the model to different starting date (d_{t0}), July 1st for the southernest site and the July 15th as an average date for all the sites.

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

2.2.3.2. Submodel for the adults flights. In order to simulate the 10 % and the 50 % of each generation, we made the three following assumptions:

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

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

At the same time we also tested different sets of parameters (Tmin = 0 °C, 5 °C, 7 °C; Tmax = 28 °C, 33 °C) Gutierrez's et al. (2012) parameters (Tmin = 8.9 °C, Topt = 30.8 °C and Tmax = 33 °C) and some Baumgärtner's et al. (2012) parameters (Tmin = 4.5 °C) (ESM6, 7 and 8).

2.2.4. Calibration of the model

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

2.2.5. Software

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

3. Results

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

3.1. Overwintering submodel

3.1.1. Model three phases testing R, T and W models with CAL, VAL and ALL data set

As described previously we tested different versions of the submodel for the three phases of overwintering (Fig. 2): 1) different functions for temperature responses (R, T, W); 2) different starting dates of prediapause (d_{t0}) (July 1st and July 15th), 3) different ways to combine temperature (T) and photoperiod (P) responses during the diapause period, using an additive (Sum) and multiplicative (Mult) factor. The best models obtained used the T and W functions, starting on 15th July

Table 4

Comparison of the best fitting of T (Triangle) and W (Wang) simulations to represent the overwintering with CAL data and using a multiplicative factor. Parameters in **bold** are fixed parameters. Parameters with an * are from the literature (Baumgärtner et al., 2012; Briere and Pracros, 1999; Gutierrez et al., 2012). The other one are free. The models 1 and 2 have free parameters. The models 3 and 4 have the parameters fixed from the models 1 and 2 and a fixed Tmin at 4.5 °C as in Baumgärtner et al. (2012) or BAUM. The models 5 and 6 consider Gutierrez's parameters (GUT) with free day length (DL). The models 7 and 8 have fixed parameters from GUT but the DL 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 Tmax = 33 °C.

Model		TAllp (1)	WAllp (2)	TAllp_Tmin4.5(BAUM) (3)	WAllpT_min4.5(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
1 st phase Prediapause	Tmin	4.94	2.45	**4.94**	**2.45**	**8.9***	**8.9***	**8.9***	**8.9***
	Topt	18.76	14.36	**18.76**	**14.36**	**30.8***	**30.8***	**30.8***	**30.8***
	Tmax	28.19	27.69	**28.19**	**27.69**	**33***	**33***	**33***	**33***
2nd phase Diapause	Tmin	5.29	7.66	**5.29**	**7.66**	**7.1***	**7.1***	**7.1***	**7.1***
	Topt	16.23	15.04	**16.23**	**15.04**	**24.1***	**24.1***	**24.1***	**24.1***
	Tmax	21.89	22.87	**21.89**	**22.87**	**28.5***	**28.5***	**28.5***	**28.5***
	Plow	9.35	9.17	**9.35**	**9.17**	12.12	8.78	12.13	3.58
	Popt	13.05	14.25	**13.05**	**14.25**	16.23	13.04	16.46	7.72
3rd phase Post-diapause	Tmin	10.47	11.39	**4.5***	**4.5***	**4.5***	**4.5***	4.4	16.18
	Topt	10.48	11.42	**10.48**	**11.42**	**30.8***	**30.8***	**30.8***	**30.8***
	Tmax	20	20	**20**	**20**	**33***	**33***	**33***	**33***
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

(d_{t0}) and multiplying the temperature and photoperiod effects. Table 3 describes only results obtained with CAL data set with a start date (d_{t0}) on July 15th and using a multiplicative (Mult) method for combining photoperiod and temperature (for further results concerning all dates and methods, see ESM4). The best results were obtained with the Triangle and Wang approaches showing EFF values of 0.77 and 0.74 respectively (Table 3). The combination method of the functions had more impact on the results than the starting dates named (d_{t0}). Moreover, the date of entry in prediapause was coherent with Baumgärnter's values (Baumgärtner et al., 2012).

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

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

In order to provide the best set of parameters we validated the defined best models (T and W) using the validation (VAL) data set (Table 5). In contrast to CAL (39 data points), the validation data (VAL) include only 12, randomly chosen observations. For this reason, apart for a low value of EFF (0.1 and 0.08) the performance statistics for VAL are more than satisfactory, with RMSE = 8.99 and AIC = 52.7.

After a first screening the different model configurations, we calibrated T and W using all available data (dataset ALL). For both response functions EFF $>$ 0.5 (0.59 for T, 0.70 for W, respectively). Satisfactory were also the values of the RMSE (8.68 for T, and 7.47 for W, respectively) (Fig. 4). We also selected W to simulate the first flight in our model as it seems to be the more stable with all the simulations made, with fixed or free parameterization.

3.2. Submodel for the adults flights

We again tested different temperature response functions (R, W, T)

Table 5

Validation of the overwintering models ford both Triangle and Wang models with (d_{t0}) = 15th July. Best fitting for Validation tests (VAL) were made with a part of the calibration (CAL) data set. The entire data set was then tested with the ALL the data set (CAL + VAL) using cross validation. The statistical analysis use the STOT (Total sum of the data squared) RMSE (Root Mean Square Error) and EFF (efficiency of the model) (ESM3).

		STASTISTICS				
Model	Data set used	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	**0.59**	51

		STASTISTICS				
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	**0.7**	51

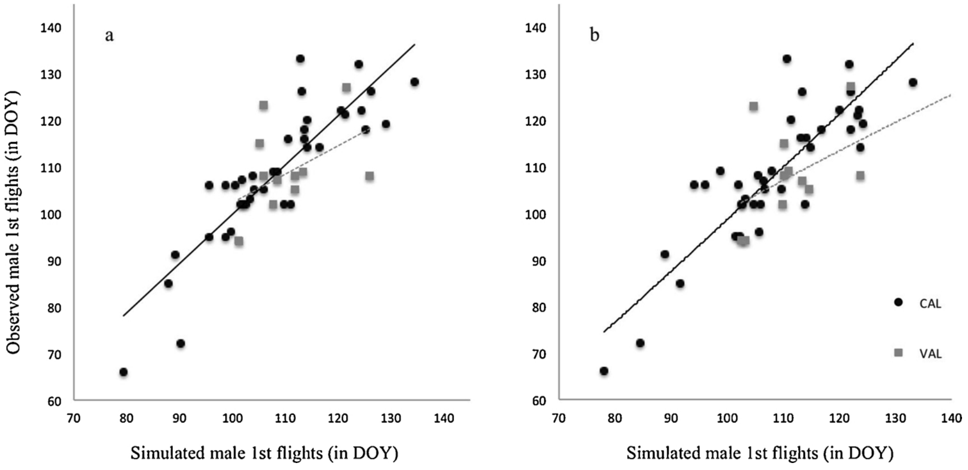


Fig. 4. Representation of the day of the first flight of *L. botrana* male with a (d_{t0}) = 15th of July and a multiplicative factor: a) Triangle model b) Wang model. Simulated and observed data in DOY (Julian days) show the quality of the simulation for each data set where CAL are in black circle and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

Table 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 Tmin = 8.9 °C, Topt = 30.8 °C and Tmax = 33 °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				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				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				27.96	0.25
W ParAllp (VAL)		VAL	46	11.15	0.84

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 Table 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.

The three models in Table 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 (Table 7).

Results obtained in Table 7 show that the models simulate correctly the 10–10 % and the 50–50 % generations when we consider parameters from the first calibration (Table 6) and with all parameters free but separating 10–10 % and 50–50 % in different datasets (for parameters values see in ESM3). The EFF was around 0.92 and 0.94 and the RMSE between 7 and 8 days for the three functions (R, T and W). Indeed, when using Gutierrez's parameters, the R and T models showed good results (EFF = 0.92), which was not the case for the W model that degraded (EFF = 0.21 and 0.26). This analysis confirms the robustness of the model and its parameters, allowing to use a single function to simulate all the generations of one cycle for the 10 to 10 % and 50 to 50 % values for each generation.

Table 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	10–10	93	8.12	0.93
R ParCal Allp			8.26	0.93
R ParGUT			8.81	0.92
R 50–50 %		**Nb data**	**RMSE**	**EFF**
R Allp	50–50	93	7.77	0.94
R ParCal Allp			7.87	0.94
R ParGUT			9.06	0.92
T 10–10 %		**Nb data**	**RMSE**	**EFF**
T Allp (10–10 %)	10–10	93	8.17	0.93
T ParCal Allp			8.31	0.93
T ParGUT			8.79	0.92
T 50–50 %		**Nb data**	**RMSE**	**EFF**
T Allp (50-50 %)	50–50	93	7.72	0.94
T ParCal Allp			7.81	0.94
T ParGUT			9.03	0.92
W 10–10 %		**Nb data**	**RMSE**	**EFF**
W Allp (10–10 %)	10–10	93	8.11	0.93
W ParCal Allp			8.33	0.92
W ParGUT			26.14	0.26
W 50–50 %		**Nb data**	**RMSE**	**EFF**
W Allp	50–50	93	7.74	0.94
W ParCal Allp			7.86	0.94
W ParGUT			27.77	0.21

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

10 %–50 % within a generation itself			Statistics	
Model R 10–50 %	**Nb data**	**Data set**	**RMSE**	**EFF**
R CAL Allp	107	CAL	5.59	0.99
R CAL ParCAL_Allp10-10			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	107	CAL	5.53	0.99
T CAL ParCAL_Allp10-10			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	107	CAL	5.55	0.99
W CAL ParCAL_Allp10-10			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

3.2.2. *Simulation 10 %–50 % of adults flights within a generation itself*

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

Results described in Table 8 show that very high values of EFF (from 0.98 to 0.99) were obtained irrespective of the model configuration. Fixing parameters for the W model to the values suggested by Gutierrez et al. (2012) significantly degraded the results (EFF = −0.05). In line with the previous tests, the sensitivity of these models have been tested fixing some parameters (Tlow/Tmin and Tmax in ESM5 and 6). All the parameters found are close to the ones known in the literature so we kept them fixed (Tmin = 8.9 °C, Topt = 30.8 °C and Tmax = 33 °C in GUT or Tmin = 4.5 °C in Baumgärtner et al. (2012)). In the first simulations with CAL data set and using free parameters (All parameters free), W seems to achieve better performances than T and R. Indeed, with fixed parameters the results did not improve with an RMSE around 5.5 days for the 3 functions and with parameters whose values are close to those found in the literature. We also validated the best model (All parameters free model) with the independent VAL dataset and we obtained good efficiency values for all the models (EFF = 0.96) and an error of 9.84 days (RMSE). Fig. 5 illustrates the distribution of the simulated and observed data for the 10–50 % of male flights within the same generation for the Wang model. The figure shows the good capacity of the model to simulate this phase. In general Fig. 6, the box size is proportional to the number of data and shows that the error for the simulation of all the generations for all the transect study have a small error (mean of +/- 5 days) between simulated and observed data.

4. General discussion of the results

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

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

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

Another issue raised in our study was to integrate the photoperiod in a large latitudinal transect (from Lat.36.710°N to Lat.48.213°N) and understand its interaction with temperatures (as multiplicative or additive factor). The analysis of this interaction (Table 3 and 4) showed that the multiplicative approach was better adapted to describe these interactions than the additive approach proposed by Baumgärtner et al. (2012) (ESM2). In any case, the multiplicative approach is the one commonly implemented in complex models and usually performs accurately (Briere and Pracros, 1998; Wang and Engel, 1998; Baumgärtner et al., 2012). Finally, the analysis also indicated that assuming a common diapause starting date, (d_{t0}) = July 15th, for the entire transect was a reasonable choice.

We show that LGM is able to correctly represent the life cycle of *L.*

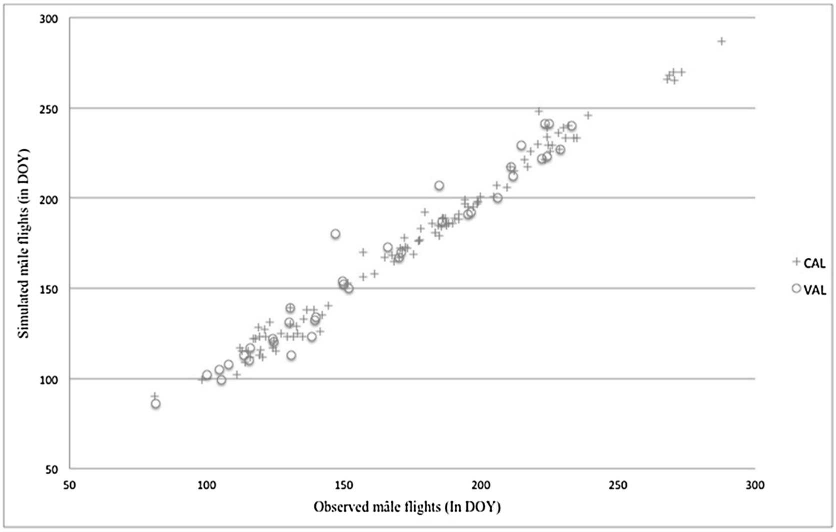


Fig. 5. Distribution of the simulated and observed data for the 10–50 % of *L. botrana* male flights within the same generation with the Wang model. Simulated and observed data show here the correlation with both the results from the calibration model (CAL with crosses) and the results from the validation model (VAL with circles).

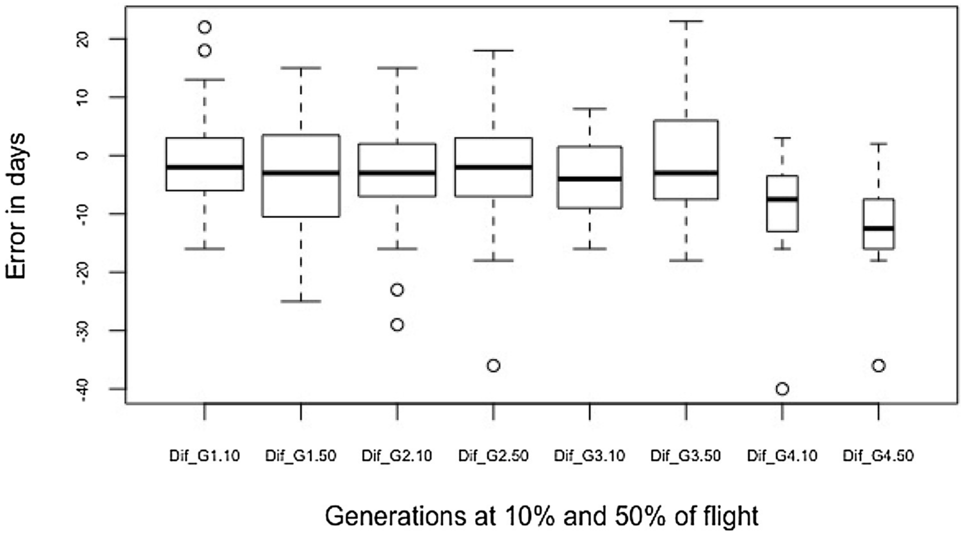


Fig. 6. Error between observation and simulations in number of days of the 10 % and 50 % of each generation of *L. botrana* flights, all site and years confounded. The errors fluctuate around 10 days before or after the observation data in the boxplots, with some extreme data, also present in the observed 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 4th generation. The size of the boxes is proportional to the number of data.

botrana in various areas with the same set of parameters, with a model performance comparable to the one of local models (Parker et al., 2011). This model is based on existing models but applied at other scale and consider less parameters that make its use easier. This approach is different to the previous one as it can be applied for large scale studies like climate change scenarios.

4.1. Proposal for a new model

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

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

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

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

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

4.2. Advantages and limits of the generic model

To define the LGM, we considered the models with the best statistical criteria and the most representative biological processes known from the literature (ESM7). One of the major difficulties we encountered was to model the overwintering phase, as we did not dispose of data to represent the associated intermediate phases (i.e., end of prediapause and end of diapause). The calibration of this complex submodel was hence performed targeting the date of the 10 % of the first generation at each site. The lack of intermediate information is a common problem faced in developing phenology models for plants (Chuine et al., 2016). In our case, the data collection have been a long process and the quality selection of the male flights had to correspond to sites where we had meteorological data available close by (at least 15 years). Some authors like Amo-Salas et al. (2011) and Armendáriz et al. (2009) integrated relative humidity in their model, but they concluded that the value error with or without this parameter was not a significant influencing factor. Indeed, we did not consider relative humidity as in Baumgärtner et al. (2012), as we did not have such data available for all our sites.

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

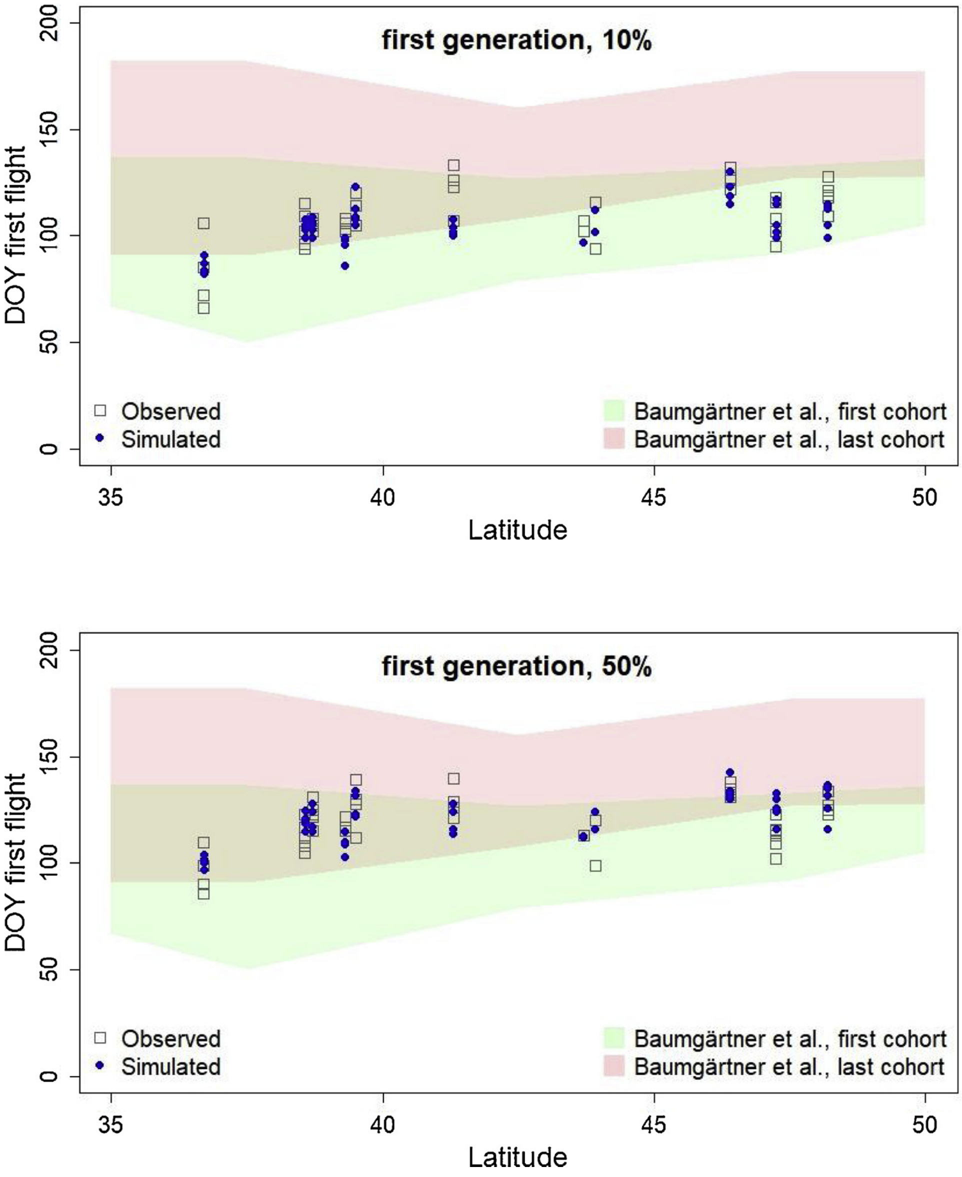


Fig. 7. Comparison between LGM observed and simulated adults flights of *L. botrana* in DOY (Day of Year) and Baumgärtner's first and last cohort observations. From a geographical perspective, both models consider a wide range of sites and climates. The simulations of G1-10 % and observations both fall within the spread of the first cohort appearing (in green) in Baugmärtner's model. The same observations can be made with the G1-50 % that fall within the spread of the last cohort appearing (in red) in Baugmärtner's model. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

obtain a stable and robust model at a large spatial scale.

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

Table 9

Final submodels selected for their efficiency according to the calibration (CAL), validation (VAL) and the full data set (ALL) of samples and the stability of their biological response to temperature. Both set of parameters obtained using the 10 % and 50 % between the generations of the *L. botrana* adults flights and the 10–10 %/50–50 % within the generations are presented. The final results for the Wang model are close to biological 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	7,49	0,74	39	9,07	0,08	12
	Dia	7,66	15,04	22,87	9,17	14,25	28,35						
	Post-dia	11,39	11,42	20,00	–	–	1,47						
W ParAllp Tmin = 4.5 °C (BAUM)	Predia	**2,45**	**14,36**	**27,69**	–	–	**39,79**	8,04	0,69	39	9,04	0,09	12
	Dia	**7,66**	**15,04**	**22,87**	**9,17**	**14,25**	**30,23**						
	Post-dia	**4,50**	**11,42**	**20,00**	–	–	**2,026**						
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

4.3. Future model applications

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

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

Author contribution statement

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

Compliance with ethical standards

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

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.ecolmodel.2020.108946.

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