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Selection of models to describe the temperature-dependent development of *Neoleucinodes elegantalis* (Lepidoptera: Crambidae) and its application to predict the species voltinism under future climate conditions

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Abstract

The small tomato borer, *Neoleucinodes elegantalis* (Guenée, 1854) is a multivoltine pest of tomato and other cultivated solanaceous plants. The knowledge on how *N. elegantalis* respond to temperature may help in the development of pest management strategies, and in the understanding of the effects of climate change on its voltinism. In this context, this study aimed to select models to describe the temperature-dependent development rate of *N. elegantalis* and apply the best models to evaluate the impacts of climate change on pest voltinism. Voltinism was estimated with the best fit non-linear model and the degree-day approach using future climate change scenarios representing intermediary and high greenhouse gas emission rates. Two out of the six models assessed showed a good fit to the observed data and accurately estimated the thermal thresholds of *N. elegantalis.* The degree-day and the non-linear model estimated more generations in the warmer regions and fewer generations in the colder areas, but differences of up to 41% between models were recorded mainly in the warmer regions. In general, both models predicted an increase in the voltinism of *N. elegantalis* in most of the study area, and this increase was more pronounced in the scenarios with high emission of greenhouse gases. The mathematical model (74.8%) and the location (9.8%) were the factors that mostly contributed to the observed variation in pest voltinism. Our findings highlight the impact of climate change on the voltinism of *N. elegantalis* and indicate that an increase in its population growth is expected in most regions of the study area.

Introduction

The small tomato borer, *Neoleucinodes elegantalis* (Guenée, 1854) (Lepidoptera: Crambidae) is one of the major pests of tomato and other cultivated crops in the neotropical region (Jordão and Nakano, 2002; Picanço *et al.*, 2007). In the larval stage, this species feeds on the fruit pulp causing severe damages that make the tomato unsuitable for marketing. In certain regions, losses of up to 90% were recorded due to outbreaks of *N. elegantalis* (Miranda *et al.*, 2005; Bortoli *et al.*, 2013). Recognizing the economic importance and the potential of this species spreading to other regions, the European and Mediterranean Plant Protection Organization (EPPO) recently listed *N. elegantalis* as a quarantine pest in Europe (EPPO, 2020). In this context, the knowledge of the factors influencing its development is of great relevance.

As in any insect, the development, survival and reproduction of *N. elegantalis* are strongly influenced by temperature (Denlinger and Yocum, 1998; Moraes and Foerster, 2015). Understanding how its development responds to temperature variations is of special interest for the applied entomology given it is an essential information in the development of phenological models (Wagner *et al.*, 1984; Rebaudo and Rabhi, 2018). In general, insects start their development from a lower thermal threshold (T_L), and their development rate increases proportionally to a temperature until reaching an optimum level (T_{opt}). At temperatures above this optimum, the development rate decreases rapidly until reaching the upper thermal threshold (T_U) (Logan *et al.*, 1976; Rebaudo and Rabhi, 2018). When insects are exposed to temperatures outside their tolerance range (below T_L and above T_U) for an extended period, their development can be drastically affected leading to the interruption of metabolic activity or even death (Marchioro *et al.*, 2017).

Due to the strong influence of temperature on insect development, the climate change expected in the coming decades may cause severe impacts on its distribution and population dynamics (Porter *et al.*, 1991). In this context, several studies have been carried out to assess the influence of climate change on agricultural and forest pests, given the potential consequences for food and wood productions (Cannon, 1998; Gilioli *et al.*, 2014; Biber-Freudenberger *et al.*, 2016; Silva *et al.*, 2017). Most of these studies investigated how climate change may affect the annual number of generations (voltinism) of insects and, consequently, their population growth (Jönsson *et al.*, 2009; Ziter *et al.*, 2012; Srinivasa Rao *et al.*, 2015, 2016; Jacques *et al.*, 2019). This information is important to predict which regions may experience an increase or a reduction in the pest population levels in the coming decades.

Mathematical models are important tools commonly applied to estimate the development rate as a function of temperature and estimate insect voltinism (Logan *et al.*, 1976; Lactin *et al.*, 1995; Briere *et al.*, 1999; Shi *et al.*, 2011; Marchioro *et al.*, 2017). Various empirical and biophysical models were developed for this purpose, and while some models describe the relationship between temperature and insect development rate as a non-linear curve (Logan *et al.*, 1976; Sharpe and DeMichele, 1977; Lactin *et al.*, 1995; Briere *et al.*, 1999), others assume a linear relationship. Once an appropriated mathematical model was selected, it can be used to simulate the development of a given species under field conditions using temperature time series data (Campbell *et al.*, 1974). Additionally, such models can also be applied to predict the changes in insect voltinism as a result of climate warming using future climate projections (Ziter *et al.*, 2012; Srinivasa Rao, *et al.*, 2016; Jacques *et al.*, 2019).

An increase of up to 4.8°C in the Earth's temperature is projected for the coming decades depending on the greenhouse gas emission rates (IPCC, 2014). A change of this magnitude in global temperatures can cause serious impacts on insect population dynamics due to the acceleration of its development rate, favouring an increase in population growth (Porter *et al.*, 1991; Srinivasa Rao *et al.*, 2015). This has important ecological and agronomical implications, including changes in interspecific interactions (Porter *et al.*, 1991; Cornelissen, 2011), introduction and establishment of invasive species into new areas (Porter *et al.*, 1991; Cornelissen, 2011) and outbreaks of agricultural pests (Jepsen *et al.*, 2008). In this context, understanding the possible impacts of climate change on the voltinism of *N. elegantalis* is relevant considering the consequences for its management. Therefore, here we assessed the effectiveness of different models in describing the temperature-dependent development rate of *N. elegantalis*. The best performance model was employed to evaluate the effects of climate warming on the pest voltinism in Southern Brazil.

Material and methods

Development rate of N. elegantalis and assessed models

Data on the development time of the immature stages and the egg–adult life cycle of *N. elegantalis* at the constant temperatures of 15, 20, 25, 27, 30 and 35°C were obtained from the literature (Marcano, 1991; Moraes and Foerster, 2015). Development data between 15 and 30°C were obtained using 120 individuals/temperature fed on tomato fruits of the hybrid cultivar 'Paronset' (Moraes and Foerster, 2015). The specimens used in the experiment were derived from a colony established with larvae collected in commercial tomato crops at the county of Almirante Tamandaré (25°19′29″S, 49°18′36″W), southeastern state of Paraná, Southern Brazil (Moraes and Foerster, 2015). The survival rate of the egg–adult life cycle ranged from 64% at 30°C to 78% at 20°C. The information that larvae do not develop at 35°C was obtained from Marcano (1991).

Table 1. Mathematical models used to describe the temperature-dependent development rate of *Neoleucinodes elegantalis*

Model	Equation[a]	Reference
Briere-1	$D(T) = aT(T - T_L)(T_U - T)^{1/2}$	Briere *et al.* (1999)
Briere-2	$D(T) = aT(T - T_L)(T_U - T)^{1/m}$	Briere *et al.* (1999)
Lactin-2	$D(T) = \mathrm{e}^{(\rho T)} - \mathrm{e}^{\left(\rho T_l - \frac{T_l - T}{\Delta}\right)} + \lambda$	Lactin *et al.* (1995)
Linear	$D(T) = a + bT$	Campbell *et al.* (1974)
Logan-6	$D(T) = \psi[\mathrm{e}^{(\rho T)} - \mathrm{e}^{(\rho T_U - (T_U T)/\Delta}]$	Logan *et al.* (1976)
Shi	$D(T) = m(T - T_L)\,[1 - \mathrm{e}^{k(T - T_U)}]$	Shi *et al.* (2011)

[a] $D(T)$ is the development rate at temperature T (°C). In the equations, T_L and T_U are, respectively, the lower and upper temperature thresholds for insect development, and the remaining parameters are fitted coefficients.

The development rate of *N. elegantalis* was calculated as the reciprocal of the development times in the different temperatures assessed. Six mathematical models previously published in the literature were selected to describe the temperature-dependent development rate of *N. elegantalis* (table 1). All model parameters were estimated with the Levenberg–Marquardt algorithm using the software Table Curve 2D (Systat, 2002).

Models' evaluation and selection

Following the methodology employed in previous studies (Roy *et al.*, 2002; Kontodimas *et al.*, 2004; Marchioro *et al.*, 2017; Jacques *et al.*, 2019), the goodness-of-fit and the models' ability to accurately estimate temperature thresholds for the development of *N. elegantalis* were used as the criteria to evaluate and select the best model. The goodness-of-fit was assessed using the standard error of regression ($S_{(e)}$) and the Akaike Information Criterion (AIC) for each model:

$$\mathrm{AIC} = n \ln\left(\frac{\mathrm{RSS}}{n}\right) + 2k$$

where n is the number of observations, RSS is the residual sum of squares, and k is the number of parameters in the model. Lower values of $S_{(e)}$ and AIC indicate a better fit of the model (Roy *et al.*, 2002; Sandhu *et al.*, 2010). ΔAIC values were obtained for each model as the difference between the AIC value calculated for a model and the lowest AIC value. Therefore, the ΔAIC of the best model is equal to zero. In this study, models with ΔAIC values lower than five were considered as having similar performances (Burnham *et al.*, 2011). Also, the accuracy of the estimated temperature thresholds was employed as an additional criterion. In this case, preference was given to models that accurately estimated temperature thresholds (T_L, T_U and T_{opt}) over those that estimate unrealistic thresholds. The accuracy was assessed based on the observed data and on the known distribution range of *N. elegantalis* (Marcano, 1991; Moraes and Foerster, 2015). Estimated thermal thresholds outside the range between 6.0 and 14.0°C for T_L, 25.0 and 34.0°C for T_{opt}, and 28.0 and 38.0°C for T_U were considered unrealistic.

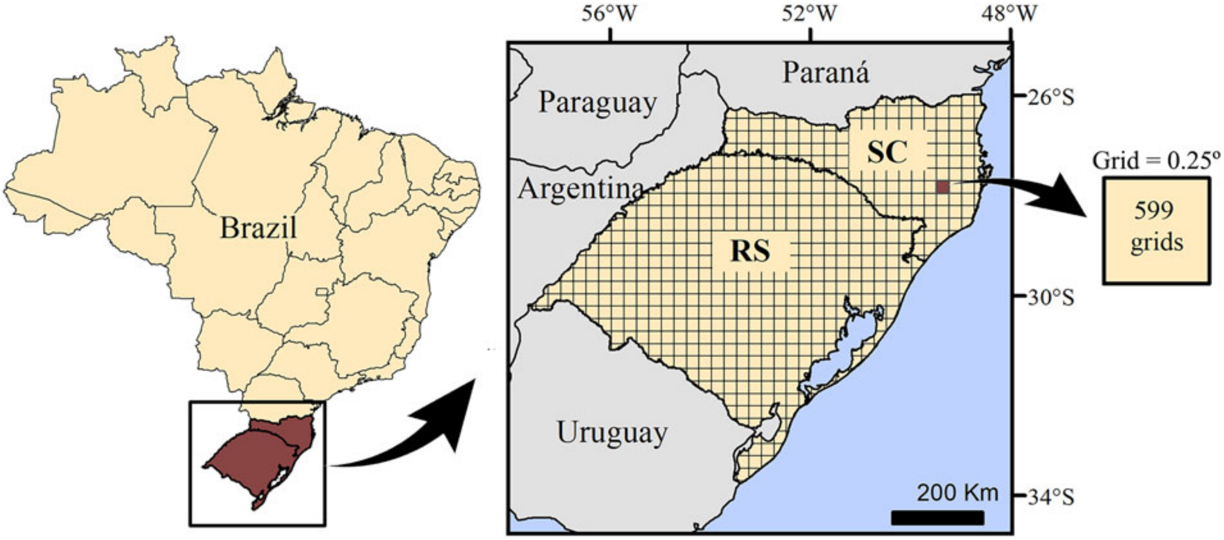

Figure 1. Study area divided into 599 grid cells of 0.25°. Voltinism was estimated under current and future climatic conditions for each of the 599 grid cells encompassing the study area (SC, Santa Catarina State; RS, Rio Grande do Sul State).

Obtaining current and future temperature data

Daily minimum and maximum air temperature data from 20 years (1994–2013) interpolated for Brazil by Xavier *et al.* (2016) were used to estimate the voltinism of *N. elegantalis* under current climate conditions. These data were obtained for a total of 599 grid cells of 0.25° comprising the States of Santa Catarina and Rio Grande do Sul, Southern Brazil (fig. 1).

Future climate data were obtained from WorldClim database in grid cells of 0.083°. This included annual mean temperature data for 2050 and 2070 based on two different climate change scenarios representing intermediate (RCP 4.5) and high (RCP 8.5) greenhouse gas emission rates derived from the Fifth Assessment Report of the IPCC (IPCC, 2014). Future climate data were obtained from three different Global Circulation Models (GCMs): CCSM4 (Community Climate System Model); HadGEM2-ES (Hadley Center Global Environmental Model version 2 Earth System) and MIROC5 (Model for Interdisciplinary Research on Climate). Consensus maps were developed by averaging the projections of the three GCMs. In order to represent current climatic conditions, annual mean temperature data were obtained between 1960 and 1990 (Hijmans *et al.*, 2005).

The methodology employed to generate future daily temperature data was described in detail by Jacques *et al.* (2019). Briefly, the difference (in °C) between future projections and current annual mean temperature was calculated to estimate the climate warming in each of the 599 grid cells comprising the study area using the data from WorldClim. This difference was added to the current daily minimum and maximum temperatures (Xavier *et al.*, 2016), generating future daily temperature data for 2050 and 2070 in the two climate change scenarios assessed.

Estimating the voltinism of N. elegantalis

The best non-linear model selected using the multiple criteria previously described and the degree-day model was employed to estimate the voltinism of *N. elegantalis*. For the non-linear model, the minimum and maximum daily temperature data were used as inputs to estimate and calculate the mean daily development rate. To obtain the annual number of generations, the daily development rates were accumulated over 1-year period.

The degree-day approach uses daily temperature data to estimate the accumulated heat units (°C) by the insect over a given T_{L}. Considering that insects require a consistent amount of heat accumulation (thermal constant) to develop from one stage to another, they can be used to estimate its number of generations within a given period (Murray, 2008). Both T_{L} and the thermal constant (K) were calculated using the coefficients of the linear model by the x-intercept method ($T_{\mathrm{L}} = -a/b$), and by the reciprocal of the slope of the regression line ($K = 1/b$), respectively (Campbell *et al.*, 1974). In this study, the average method with a horizontal cut-off was used to accumulate the degree-days, using the equation:

$$\mathrm{GDD} = \sum_{i=1}^{365} \frac{[T_{\min} + T_{\max}]}{2} - T_{\mathrm{L}}$$

where GDD is the accumulated degree-days, T_{L} is the lower temperature threshold, $T_{\min}$ is the daily minimum temperature and $T_{\max}$ is the daily maximum temperature. According to the horizontal cut-off approach, the development of *N. elegantalis* levels off when the upper threshold of 29.95°C was extrapolated. Voltinism in each of the 599 grid cells was calculated using Microsoft Excel® by dividing the degree-days accumulated over 1-year period by the thermal constant (GDD/K) (Ziter *et al.*, 2012). The Microsoft Excel spreadsheet with the voltinism data was joined to a shapefile containing the 599 grid cells comprising the study area using the 'Add join' tool in the software ArcMap 10.4 (ESRI, 2016). All maps were generated and exported as figures with the software ArcMap 10.4 (ESRI, 2016).

Partitioning analysis

An analysis of variance (ANOVA) was used to assess the contribution of the model (non-linear and degree-day), location (599 grid cells), climate change scenario (RCP 4.5 and RCP 8.5) and period (2050 and 2070) to the observed total variation in the

Table 2. Performance of the mathematical models used to describe the temperature-dependent development rate of *Neoleucinodes elegantalis* based on the standard error of the regression ($S_{(e)}$) and on the Akaike Information Criterion (AIC)

	Egg		Larvae		Pupae		Egg–adult cycle	
Model	$S_{(e)}$ (10^{-3})	ΔAIC[a]	$S_{(e)}$ (10^{-3})	ΔAIC[a]	$S_{(e)}$ (10^{-3})	ΔAIC[a]	$S_{(e)}$ (10^{-4})	ΔAIC[a]
Briere-1	13.89	7.77	5.71	5.80	**3.97**	**0.00**	19.31	15.18
Briere-2	14.57	6.78	16.48	18.10	**4.42**	**0.84**	**7.99**	**4.63**
Lactin-2	**7.79**	**0.53**	**3.65**	**0.00**	**4.89**	**2.06**	**4.90**	**0.00**
Linear	[b]	[b]	[b]	[b]	[b]	[b]	[b]	[b]
Logan-6	19.90	9.90	6.10	6.17	8.94	9.30	16.01	11.84
Shi	**7.40**	**0.00**	**3.65**	**0.01**	**4.88**	**2.03**	**4.92**	**0.05**

[a] ΔAIC is the difference between the AIC calculated for a model and the lowest AIC value. Bold ΔAIC values indicate that the models had a similar performance (ΔAIC ≤ 5).

[b] AIC values not calculated because of the differences in the number of samples compared to the non-linear models due to the exclusion of the temperatures outside the linear range between temperature and the development rate of *N. elegantalis*.

voltinism of *N. elegantalis.* To obtain the individual contribution of each source of variation, the sums of squares of each source was divided by the total sum of squares explained by all sources of variation. This analysis was performed using R (R CORE TEAM, 2015).

Results

Model assessment

Lactin-2 and Shi models were the ones that showed the best performance, consistently showing the lowest $S_{(e)}$ and ΔAIC values for all development stages evaluated (table 2, fig. 2). Furthermore, these models also estimated temperature thresholds in accordance with the expected for *N. elegantalis* (table 3). On the other hand, in addition to the comparatively poor fit, the model Briere-2 also estimated unrealistic T_L for the egg and larval stages (4.3 and −2.9°C, respectively) (table 3, fig. 2).

The estimated temperature thresholds varied widely depending on the model and the insect development stage (table 4). For example, T_L ranged between 4.3 and 11.0°C in the egg stage, −2.9 and 9.1°C in the larval stage, 7.7 and 12.0°C in the pupal stage, and between 8.2 and 10.9°C in the egg–adult life cycle. Similar variations were also observed for T_U and T_{opt}. Also, the pupal stage seems to be the one with the lowest tolerance to low temperatures, according to the estimations of most models (table 4).

Number of days in the year on which temperatures were below T_L and above T_U

The number of days in the year that daily temperatures exceeded T_U and were below T_L based on the estimations provided by Lactin-2 varied according to location, climate change scenario and years (fig. 3). The mountainous region of Santa Catarina and Rio Grande do Sul showed the highest number of days with temperatures below T_L and had comparatively fewer days with temperatures above T_U. By contrast, north-eastern Santa Catarina and western Rio Grande do Sul and Santa Catarina showed the lowest number of days with temperatures below T_L and the highest with temperatures extrapolating T_U. In general, an increase was estimated in the number of days at which temperature exceeded T_U in the scenarios with higher greenhouse gas emission rates and in 2070 compared to 2050. The opposite was recorded for the lower temperature threshold, with a reduction in the number of days at which temperature was below T_L (fig. 3). For example, while under current climate conditions, the number of days below T_L ranged between 10 and 148, in the RCP 8.5 scenario, this variation was of 10 and 77 by 2070.

Voltinism of N. elegantalis under current climate conditions

The voltinism of *N. elegantalis* was estimated using the model Lactin-2 and the degree-day approach. Lactin-2 was selected based on its good performance, and because it is one of the most used non-linear models for describing the temperature-dependent development rate of several species (Rebaudo *et al.*, 2018). The annual number of generations estimated by the models using current temperature data varied widely across regions, and this variation was more prominent in the predictions provided by the degree-day model (fig. 4). Lactin-2 and the degree-day model estimated up to seven and eight generations in the warmer regions comprising the coastal region of Santa Catarina and north-eastern Rio Grande do Sul, respectively, while only four generations were estimated in the colder regions (mountainous region of Santa Catarina and Rio Grande do Sul).

Climate change and voltinism of N. elegantalis

The number of generations estimated with the degree-day model ranged from 4.9 to 8.7 in the RCP 4.5 scenario for 2050 and between 5.1 and 8.9 for 2070. In the scenario RCP 8.5, this variation was 5.1 and 8.9 in 2050 and 5.7–9.3 in 2070. Using the Lactin-2 model, a variation of 4.9–7.2 generations was estimated in the scenario RCP 4.5 for 2050, and between 5.0 and 7.2 generations for 2070. The number of generations ranged from 5.0 to 7.3 in 2050 and from 5.2 to 7.1 in 2070 in the scenario RCP 8.5 (fig. 4).

In general, both models estimated an increase in the number of generations of *N. elegantalis* in the different climate change scenarios and years evaluated, but the magnitude of this increase varied mainly depending on the model and location (fig. 5). Both models predicted a greater increase in voltinism in the areas that currently show mild and cold temperatures. However, while the degree-day model estimated an increase in the voltinism of *N. elegantalis* in the entire study area, Lactin-2 predicted only a subtle increase or even a decrease in the number of generations in regions where temperature more often exceeded the species'

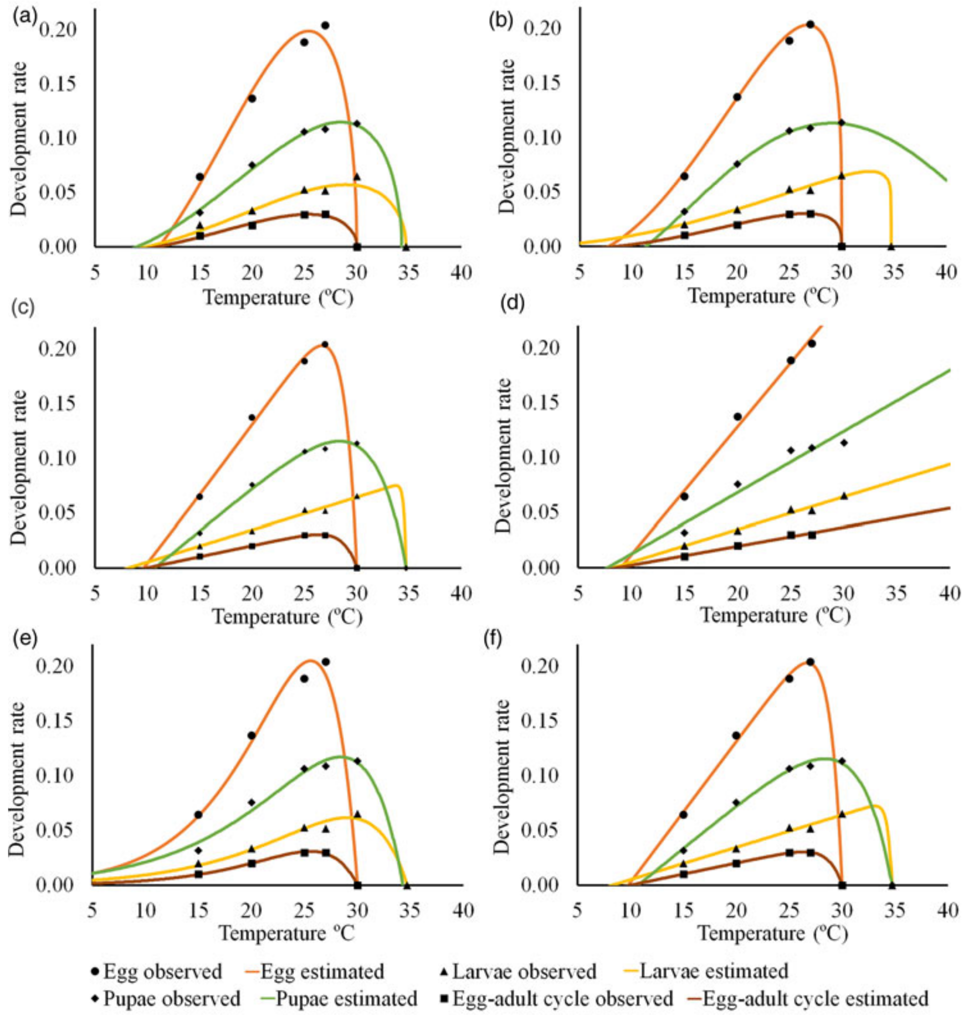

Figure 2. Fitting of the mathematical models used to describe the temperature-dependent development rate of *Neoleucinodes elegantalis* for the egg, larval, pupal stages and egg–adult life cycle. Equations are: (a) Briere-1; (b) Briere-2; (c) Lactin-2; (d) Linear; (e) Logan-6; and (f) Shi.

Table 3. Number of temperature thresholds estimated by each model used to describe the temperature-dependent development rate of *Neoleucinodes elegantalis*, and their accuracy inferred based on the observed development times and on the known species distribution range

Models	Number of estimated temperature thresholds	Accuracy[a]		
		T_L	T_{opt}	T_U
Briere-1	3	+	+	+
Briere-2	3	–	+	+
Lactin-2	3	+	+	+
Linear	1	+	•	•
Logan-6	2	•	+	+
Shi	3	+	+	+

[a] +, yes; –, no; •, parameter not estimated by the model.

upper thermal threshold (fig. 5). These regions included mainly northeastern and western Santa Catarina and north and southeast of Rio Grande do Sul.

Variation partitioning

The mathematical model was the main factor explaining the variation in the voltinism of *N. elegantalis* (74.8%), followed by location (9.8%) and the interaction between model and location (12.6%). Overall, 98.7% of the observed variation in voltinism was explained by these two factors and their interaction.

Discussion

Predictions of climate change for the coming decades indicate that Earths' temperature may increase by up to 4.8°C above pre-industrial levels depending on the greenhouse gas emission rate (IPCC, 2014). In this context, understanding how the development of ectotherm organisms is affected by temperature is essential to anticipate the impacts of climate change and may have practical applications in the case of economically important species such as *N. elegantalis*. Also, although climate change is a global event, the velocity of changes in temperature is not expected to be uniform across regions (Loarie *et al*., 2009), and therefore the response of insects to climate warming should be considered as locally dependent.

The first step in predicting the impacts of climate change on insect voltinism is the understanding of how their development

Table 4. Parameter values of each phenological model and development stages of *Neoleucinodes elegantalis*

Model	Parameters[a]	Egg	Larvae	Pupae	Egg–adult cycle
Briere-1	$a(10^{-5})$	25.500	4.308	8.123	3.804
	T_{L}	11.060	9.092	8.513	10.885
	T_{U}	30.000	34.700	34.700	30.000
	T_{opt}	27.650	29.750	29.250	25.750
Briere-2	$a(10^{-5})$	28.292	5.495	7.759	4.212
	m	5.483	8.933	1.784	3.167
	T_{L}	4.319	−2.881	9.429	8.237
	T_{U}	30.000	34.700	34.700	30.000
	T_{opt}	27.650	33.700	28.350	25.250
Lactin-2	$\rho(10^{-3})$	4.364	1.063	2.797	0.733
	Δ	1.173	0.203	3.173	1.349
	T_{l}	32.905	35.430	43.454	35.707
	λ	−2.834	−2.741	−2.800	−2.737
	T_{L}	9.600	8.200	12.000	9.950
	T_{U}	30.050	34.650	42.200	29.950
	T_{opt}	28.250	33.950	28.400	27.050
Linear	$a(10^{-2})$	−10.452	−2.446	−4.306	−1.491
	$b(10^{-3})$	11.636	2.960	5.570	1.722
	T_{L}	8.982	8.262	7.732	8.662
	K	85.940	337.807	179.547	580.804
Logan-6	p	0.226	0.175	0.164	0.224
	Δ	4.415	5.670	6.050	4.453
	ψ	0.152	0.056	0.041	0.073
	T_{U}	30.013	34.718	34.696	30.009
	T_{opt}	26.500	29.900	28.650	25.800
Shi	k	0.823	2.657	0.279	0.690
	$m\ (10^{-3})$	0.012	0.002	7.896	0.002
	T_{L}	9.794	8.261	10.715	9.938
	T_{U}	31.213	35.076	38.280	31.447
	T_{opt}	27.400	33.350	29.700	27.050

[a] T_{L}, T_{U}, T_{opt} and K are, respectively, the lower temperature threshold, upper temperature threshold, the optimum temperature for development and the thermal constant. The remaining parameters are fitted coefficients.

responds to temperature variations, and for this purpose, the selection of models for describing the relationship between temperature and development rate is essential. Here, following literature recommendations, we tested several functions and used a multiple criteria methodology to select the best model to describe the response of *N. elegantalis* to temperature (Kontodimas *et al.*, 2004; Marchioro *et al.*, 2017; Quinn, 2017; Jacques *et al.*, 2019). The best model was selected considering the reliability of the estimated temperature thresholds in addition to the commonly used statistical metrics such as goodness-of-fit. Based on these criteria, Lactin-2 and Shi had the best performance, as both models showed a good fit to the observed data in all development stages and estimated adequate temperature thresholds for *N. elegantalis*. Since it was published in 1995, the model Lactin-2 has been one of the most employed functions in modelling studies (Rebaudo *et al.*, 2018) and has been shown suitable for several species (Roy *et al.*, 2002; Kontodimas *et al.*, 2004; Karimi-Malati *et al.*, 2014). On the other hand, the model developed by Shi *et al.* (2011) is more recent and to date few studies evaluated its performance (e.g. Marchioro *et al.*, 2017; Jacques *et al.*, 2019). There are numerous equations used for modelling the temperature-dependent development of insects and the fact that their performance may vary according to species reinforces the importance of evaluating several models in the selection process before using them for climate change modelling or pest management purposes, as pointed out by other studies (Quinn, 2017; Rebaudo and Rabhi, 2018; Jacques *et al.*, 2019).

Because the predictions of voltinism may vary depending on the mathematical model (Jacques *et al.*, 2019), here we estimated the annual number of generations of *N. elegantalis* using two

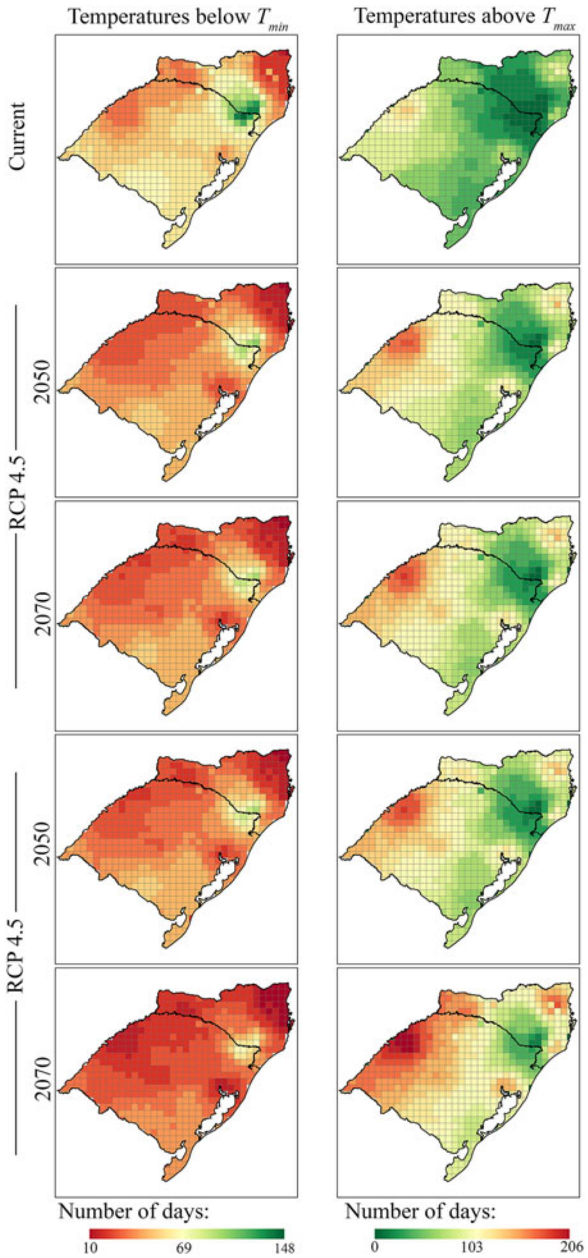

Figure 3. Number of days in the year that temperatures were below the lower temperature threshold (9.9°C) and above the upper temperature threshold (29.9°C) estimated for *Neoleucinodes elegantalis* in southern Brazil.

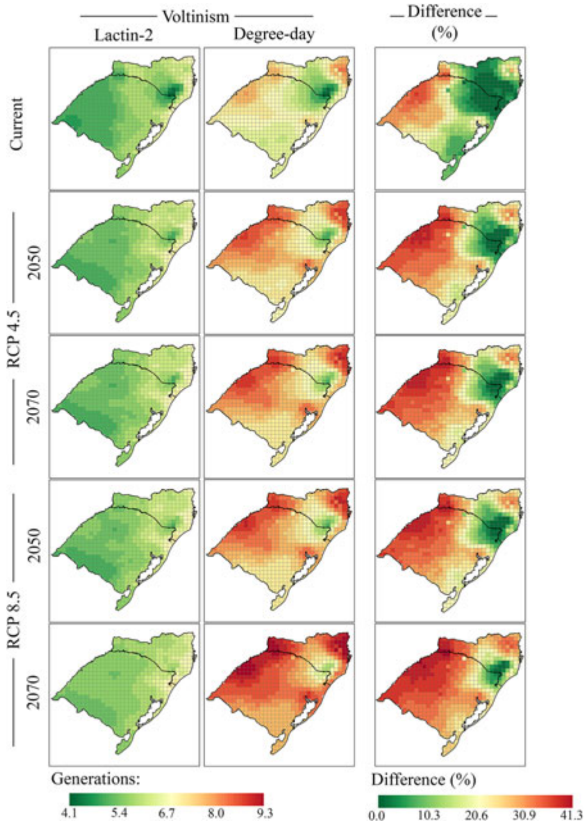

Figure 4. Comparison of *Neoleucinodes elegantalis* voltinism estimated with non-linear (Lactin-2) and degree-day models in different years and climate change scenarios in Southern Brazil.

models based on different assumptions. While Lactin-2 considers that the relationship between temperature and insect development rate is non-linear over the temperature range tolerated by the species, the degree-day assumes that this relationship is linear. Furthermore, the non-linear model assumes that the development rate ceases when T_{U} is extrapolated, while the horizontal cut-off used in the degree-day model considers that it levels off (Murray, 2008). Although both models have estimated a similar pattern in voltinism with colder regions showing fewer generations than the warmer ones, the models' specificities generated marked differences in the estimations. For example, differences of up to 36% were recorded between Lactin-2 and the degree-day model under current climate conditions, and this difference increased to 41% by 2070 in the RCP 8.5 scenario. Also, differences between model predictions were locally dependent, and tended to be more significant in the warmer regions. This can be explained by the relatively low T_{U} estimated for *N. elegantalis*, and also by differences in how the models estimate the development rate in temperatures above T_{U}, especially in the case of future projections when it is expected that temperatures extrapolate T_{U} more often.

The differences in the models' assumptions also influenced the future projections of voltinism change. The predictions provided by the degree-day model indicate an increase in the voltinism in the entire study area, while decreases in voltinism were estimated in certain regions by Lactin-2. Although a similar result was recorded in a study comparing the changes in voltinism of *Mythimna sequax* (Lepidoptera: Noctuidae) under future climate scenarios in Southern Brazil (Jacques *et al.*, 2019), the regions where a reduction in voltinism was estimated varied between both studies. This occurred due to marked differences in the temperature thresholds estimated for *M. sequax* and *N. elegantalis*. For example, a difference of 3.5°C was recorded between the lower thermal threshold estimated for *M. sequax* (6.4°C) and *N. elegantalis* (9.9°C). Similarly, for the upper thermal threshold, a variation of 2.1°C was observed between the threshold of 32°C estimated for *M. sequax* and 29.9°C for *N. elegantalis*. The observed variation between studies in the estimations of voltinism changes demonstrates that the choice of models can result in significant differences in future predictions. These findings reinforce the need to consider the differences among models in order to select the one that best represents the biology of the species under study (Roltsch *et al.*, 1999).

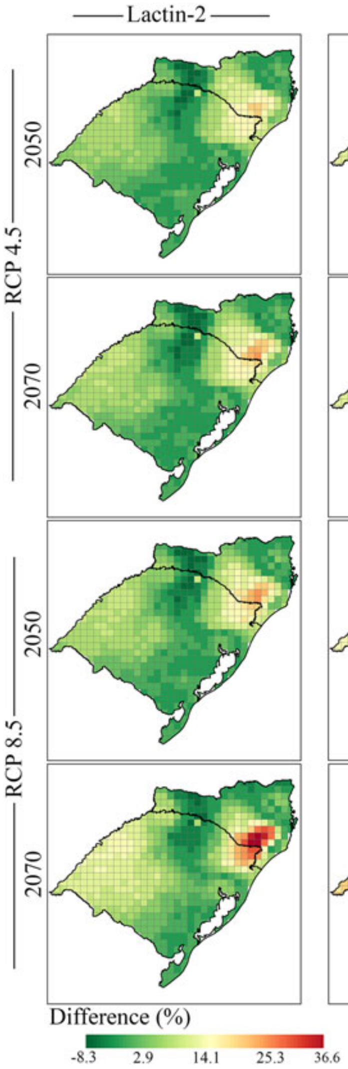

Figure 5. Difference in percentage between current and future number of generations of *Neoleucinodes elegantalis* using non-linear (Lactin-2) and degree-day models in southern Brazil. While negative values indicate a decrease in the number of generations, positive values indicate an increase.

In addition to the models, location also provided a major contribution to the variation in voltinism, as demonstrated by the ANOVA. This result can be explained by the climate heterogeneity of Southern Brazil, characterized by colder areas that experience frequent frost in winter and temperate summers, and also regions with mild winters and warm summers (Alvares *et al.*, 2013). Similar results regarding the importance of location in the variation of voltinism were found by other studies carried out with different insect species (Ziter *et al.*, 2012; Srinivasa Rao *et al.*, 2015, 2016; Jacques *et al.*, 2019). For example, a study found that location explained on average 33% of the total variation in the voltinism of 13 insect pests in California (Ziter *et al.*, 2012). Similarly, for *Helicoverpa armigera* (Hubner) (Lepidoptera: Noctuidae), *M. sequax* and *Spodoptera litura* Fab. (Lepidoptera: Noctuidae) location explained 65, 37 and 35% of the variation in the voltinism, respectively (Srinivasa Rao *et al.*, 2015, 2016; Jacques *et al.*, 2019).

The predicted changes in voltinism for the coming decades may affect the population growth of *N. elegantalis*, with potential consequences for crop production. Although other life-history traits that affect insect population dynamics were not assessed in this study (e.g. survival rate, reproduction), the voltinism can be considered a determinant factor for population growth (Porter *et al.*, 1991). In this context, the population growth of *N. elegantalis* may be favoured in regions predicted to face an increase in voltinism. These regions include mainly the high-altitude areas currently showing low and mild temperatures (e.g. mountainous Santa Catarina and Rio Grande do Sul) where an increase in voltinism of up to 37% was predicted in the RCP 8.5 scenario by 2070 by both models. Tomato and other solanaceous plants used as host by *N. elegantalis* are cultivated throughout the study area, and the increase in its population levels may cause severe damages on crops and therefore higher yield losses. In addition to damages on crops, the greater number of generations accelerates the selection of genotypes resistant to pesticides (Maino *et al.*, 2018; Pu *et al.*, 2019), which may hamper the control of *N. elegantalis* and increase production costs in the medium and long term.

In summary, this study selected among six models the ones that best describe the relationship between temperature and development rate of *N. elegantalis*. The best models selected using a multiple criteria process were Lactin-2 (Lactin *et al.*, 1995) and Shi (Shi *et al.*, 2011). Lactin-2 was used to estimate the species' voltinism under two different climate change scenarios and time periods and these predictions were compared to those provided by the commonly used degree-day method. Markedly, differences were observed between the predictions of the Lactin-2 model and the degree-day, especially in the warmer regions. Additionally, while Lactin-2 predicted a decrease in the number of generations in certain regions (e.g. north-eastern and western Santa Catarina and north and southeast of Rio Grande do Sul), the degree-day model estimated an increase in voltinism in the entire study area. Our study provides an important contribution to the understanding of how *N. elegantalis* respond to temperature, and these findings can be applied to the management of this important pest and to assess the potential impacts of climate change on its population growth.

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