Modeling temperature-dependent survival with small datasets: insights from tropical mountain agricultural pests

**Verónica Crespo-Pérez[1,2,3,5]*, Olivier Dangles[1,2,3],
Jacques Régnière[4] and Isabelle Chuine[5]**

[1]IRD, UR 072, Diversité, Ecologie et Evolution des Insectes Tropicaux,
Laboratoire Evolution, Génomes et Spéciation, UPR 9034, CNRS, 91198
Gif-sur – Yvette Cedex, France: [2]Université Paris-Sud 11, 91405 Orsay Cedex,
France: [3]Laboratorio de Entomología, Facultad de Ciencias Exactas y
Naturales, Pontificia Universidad Católica del Ecuador, 12 de Octubre, 1076 y
Roca, Quito, Ecuador: [4]Natural Resources Canada, Canadian Forest Service,
Laurentian Forestry Centre, PO Box 10380 Stn. Ste Foy, Quebec, QC, Canada
G1V 4C7: [5]Centre d'Ecologie Fonctionnelle et Evolutive, CNRS, 1919 route de
Mende, 34293 Montpellier cedex 5, France

Abstract

Many regions are increasingly threatened by agricultural pests but suffer from
a lack of data that hampers the development of adequate population dynamics
models that could contribute to pest management strategies. Here, we present a new
model relating pest survival to temperature and compare its performance with two
published models. We were particularly interested in their ability to simulate the
deleterious effect of extreme temperatures even when adjusted to datasets that did
not include extreme temperature conditions. We adjusted the models to survival data
of three species of potato tuber moth (PTM), some major pests in the Tropical Andes.
To evaluate model performance, we considered both goodness-of-fit and robustness.
The latter consisted in evaluating their ability to predict the actual altitudinal limits of
the species in the Ecuadorian Andes. We found that even though our model did not
always provide the best fit to data, it predicted extreme temperature mortality and
altitudinal limits accurately and better than the other two models. Our study shows
that the ability to accurately represent the physiological limits of species is important
to provide robust predictions of invasive pests' potential distribution, particularly in
places where temperatures approach lethal extremes. The value of our model lies
in its ability to simulate accurate thermal tolerance curves even with small datasets,
which is useful in places where adequate pest management is urgent but data are
scarce.

Keywords: Agricultural pests, *Phthorimaea operculella*, potato tuber moth,
Symmetrischema tangolias, *Tecia solanivora*, temperature-related survival

*Author for correspondence
Phone: (593) 22991700, ext. 1294; Fax: (593) 22991687
E-mail: mvcrespo@puce.edu.ec

Introduction

Developing countries in tropical regions face considerable losses in their agricultural economy because the unmarked seasonality of their climate allows pests to thrive and propagate more easily than in temperate countries (Nyssen *et al.*, 2009). Mountainous tropical regions show high environmental heterogeneity that promotes niche partitioning and increases the higher risk of invasion by successively introduced pest species (Duyck *et al.*, 2006; Geurts *et al.*, 2012). Most studies of temperature-dependent process rates in insect pests have concerned temperate regions (Gilbert *et al.*, 2004; Hodkinson, 2005; Logan *et al.*, 2007). Tropical regions have received little attention although they represent important places for agriculture development (Nyssen *et al.*, 2009; Young, 2009). There is thus an urgent need for accurate and efficient risk assessment tools that will allow governments to focus their management efforts on the most vulnerable sites (Perez *et al.*, 2010).

A species' fitness in a particular ecosystem depends on its responses to environmental conditions. Survival probability is an important component of fitness that reflects the level of tolerance of organisms to the environment (Gilchrist, 1995). Survival of ectotherms, such as insects, is mainly influenced by temperature and occurs within a definite temperature range, with an optimum between high and low lethal temperatures (Angilletta, 2009). Temperature-related survival is commonly modeled with tolerance curves, which are useful within insect pest management programs as they allow the identification of vulnerable sites when coupled to temperature regimes that occur in a particular landscape (Logan *et al.*, 2007). The objective of this study was to compare the performance of three models to simulate the temperature-related survival of the immature stages of three species of invasive potato tuber moth (PTM), *Phthorimaea operculella* (Zeller), *Symmetrischema tangolias* (Gyen), and *Tecia solanivora* (Povolny), when parameterized with a limited number of data. Unlike many temperate regions where studies benefit from increasingly abundant experimental and observational data (Luo *et al.*, 2011 and other publications from the same issue), the tropical Andes lack sufficient data on many pest species threatening their agricultural landscapes. Data on extremely lethal temperatures are often absent, which is frequently a drawback for accurate modeling of species survival rates (Niño, 2004; Sporleder *et al.*, 2004; Jaramillo *et al.*, 2009). We were particularly interested in evaluating the ability of the models to predict the deleterious effect of temperature even when fitted to datasets that do not include data on lethal temperatures.

Study system

Within the last 30 years *P. operculella*, *S. tangolias*, and *T. solanivora* have been invading the potato fields of the Northern Andes and represent today one of the most serious agricultural pest problems in the region (Dangles *et al.*, 2010). These three species seem to differ in their physiological responses to temperature (Dangles *et al.*, 2008), which play an essential role in defining their geographic distribution along the environmentally heterogeneous Northern Andean landscapes. They have been observed co-occurring in some places of Colombia and Ecuador, even within the same potato storage structure or sack (Dangles *et al.*, 2008). The degree of damage to field or stored potato depends on which species are present and on the sequence of invasion. Since they have proven to respond differently to control strategies (Sporleder *et al.*, 2005; Rebaudo *et al.*, 2006) their co-existence may complicate the establishment and success of control tactics. Integrated pest management of these pests will therefore greatly benefit from a thorough understanding of their thermal niches.

Materials and methods

The models

The first model we tested was Sharpe & DeMichele's model (Sharpe & DeMichele, 1977, modified by Schoolfield *et al.*, 1981) originally developed to describe poikilotherm development rate. Although widely used to model ectotherm development, for example, that of the PTM *P. operculella* (Sporleder *et al.*, 2004), its numerous parameters may be difficult to estimate from a small number of data points covering a narrow range of temperatures. The second model we evaluated was a second-order polynomial function used by Sporleder *et al.* (2004) to describe the mortality rate of *P. operculella*. Even though these authors managed to fit it fairly well to their data, this model may fail to produce the unimodal shape typical of survival curves. Finally, we tested a model developed by Régnière *et al.* (2012). This model takes into account the simultaneous effects of temperature on survival rate and development time that determine the overall survival relationship to temperature.

Data compilation

To study the influence of temperature on survival of the immature stages (egg, larva, and pupa) of the three species of PTM we collated published data of laboratory experiments performed in the Andean region (table 1). From these sources, only data acquired under constant temperatures (±2°C) were considered. In all studies, relative humidity ranged from 60 to 90%.

Modeling survival

Temperature-related survival of ectotherms has been shown to have a parabolic shape, with low survival at low and high temperatures (fig. 1) (van der Have, 2002). In this study, we assess the performance and robustness of three different models for simulating this type of response in PTM.

Sharpe and DeMichele's model

This model was developed by Sharpe & DeMichele (1977) to describe the kinetics of insect development based on several assumptions about the underlying developmental control enzymes. It has been widely used to describe poikilotherms' temperature-dependent development (Gilbert *et al.*, 2004). We decided to include Sharpe and DeMichele's model (as modified by Schoolfield *et al.*, 1981) in our study because of its biological significance and because it has been successfully used to simulate tuber moth development and survival

Table 1. Survival and development time data at several constant temperatures for immature stages of the three species of PTM obtained from several published sources.

Species	Data source	Temp	Eggs		Larvae		Pupae	
			Dev. time (days)	Survival %	Dev. time (days)	Survival %	Dev. time (days)	Survival %
P. operculella	Sporleder *et al.* (2004)	10.6	35.5	77.8	106.7	14.8		
		10.7					48.0	58.3
		15.0	16.4	86.7				
		16.0					29.7	91.2
		16.1	12.1	82.8	58.1	50.5		
		20.3	8.1	85.8	25.1	68.5	12.2	94.6
		23.0	6.2	86.0	16.7	76.2	9.6	88.9
		24.0	5.5	91.0	17.6	80.5		
		25.0			16.7	76.0	8.4	86.7
		26.1	4.9	88.0				
		26.2					8.2	92.3
		26.3			14.6	88.5		
		26.5					8.8	91.7
		26.7	5.1	84.5				
		28.0			11.6	67.0		
		30.0			10.1	77.8		
		30.2					6.2	92.2
		31.0	3.8	88.9				
S. tangolias	Dangles *et al.* (2008)	10.0	38.8	60.0	108.3	60.0	79.2	68.0
		15.0	13.7	81.0	47.4	69.0	26.6	85.2
		20.0	10.5	81.6	30.8	69.6	18.9	86.0
	Palacios *et al.* (1998)	12.6	16.0	96.0	58.0	72.0	32.0	74.0
		13.0	17.0	88.0	57.0	54.0	31.0	82.0
		17.4	9.0	69.0	40.0	72.0	22.0	85.0
T. solanivora	Dangles *et al.* (2008)	10.0	32.9	55.8	71.3	45.0		
		15.0	17.3	84.0	41.9	80.0	23.3	90.6
		20.0	10.0	88.0	20.6	90.0	17.6	92.0
	Torres *et al.* (1997)	20.0	7.0	71.9	17.3	56.0	11.0	70.6
		25.0	5.0	44.4	14.7	28.0	9.9	80.0
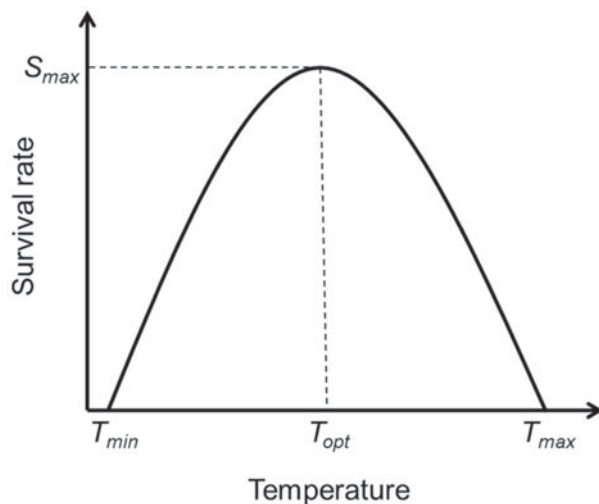
Fig. 1. General shape of the relationship between survival rate and temperature, with an optimum temperature, T_{opt}, where survival rate is maximized (S_{max}), and a minimum and a maximum temperature (T_{min} and T_{max}) at which survival rate is zero.

in other studies (Roux, 1993; Sporleder *et al.*, 2004). The equation of survival is:

$$s(T) = \frac{\frac{dT}{298.16}\exp\left[\frac{e}{R}\left(\frac{1}{298.16} - \frac{1}{T}\right)\right]}{1 + \exp\left[\frac{f}{R}\left(\frac{1}{g} - \frac{1}{T}\right)\right] + \exp\left[\frac{h}{R}\left(\frac{1}{i} - \frac{1}{T}\right)\right]} \quad (1)$$

with T mean temperature expressed in K, R the universal gas constant (1.987 cal.K^{-1}.mol^{-1}), and d, e, f, g, h, and i parameters to be estimated (see the 'Model parameterization' section below).

Sporleder's polynomial model

Sporleder *et al.* (2004) described the relation between mortality rate $M(T)$ and temperature for different life stages of *P. operculella* with a second-order polynomial function of the form:

$$M(T) = m_1 T^2 + m_2 T + x, \quad (2)$$

where m_1, m_2, and x are parameters to be estimated. While second degree polynomials are appropriate to describe

a parabolic relationship they usually provide a poor extrapolation beyond the range of observations. Nevertheless, we decided to test this rather simple model on survival data of the three species of PTM because it had already been used to simulate mortality of one of the species of PTM (Sporleder et al., 2004). To model the survival data, we expressed survival rate as the inverse of mortality rate:

$$s(T) = 1 - M(T). \tag{3}$$

Régnière's model

Régnière et al. (2012) assume that the survival rate $s(T)$ at a given temperature T is constant throughout a life stage, and that the overall probability of survival during the life stage is simply a matter of exposure duration $\bar{t}_T$ (the average stage duration at temperature T) to that temperature-dependent survival rate. Here, a second-degree polynomial logistic model was used to describe $s(T)$, the relationship between survival rate and temperature, yielding:

$$s(T) = \left(\frac{1}{1 + e^{a+bT+cT^2}}\right)^{\bar{t}_T} \tag{4}$$

with a, b, and c parameters to be estimated. To obtain a continuous description of the relationship between temperature and stage-specific survival, it is necessary to replace $\bar{t}_T$ in equation (4) by the development-time response function $\tau(T)$ to temperature of each life stage and species. For this, we fitted the Sharpe–Schoolfield model (Schoolfield et al., 1981) to mean development time data, by the maximum likelihood method of Régnière et al. (2012).

Model parameterization

Parameters of the three models were estimated using log-likelihood assuming that the number of survivors out of the initial number in each treatment is binomially distributed, with $s(T)$ representing survival probability. Some of the datasets of S. tangolias were incomplete and lacked information about sample sizes. In those cases, in order to parameterize our models, we assumed an arbitrary number of 100 individuals. Parameters of the development-time response function, $\tau(T)$, of the three life stages of the three species are given in Appendix 1 in Supplementary material.

Model evaluation

We used the Bayesian Information Criterion (BIC) (Schwarz, 1978) to compare the performance of the three models within each immature stage of each species:

$$\text{BIC} = (-2^*LL) + (k^*\text{Ln}(n)), \tag{5}$$

where LL is log-likelihood of the model, k is the number of parameters in the model, and n is sample size (i.e. number of data points). BIC allows classifying models according to their performance, the model showing the smallest value of BIC being the best. We also computed posterior model probability (Raftery, 1995; Burnham & Anderson, 2004), which is the probability of the model being correct for the data:

$$p_i = \text{Pr}\{g_i | \text{data}\} = \frac{\exp\left(-\frac{1}{2}\Delta \text{BIC}_i\right)}{\sum_{r=1}^{R} \exp\left(-\frac{1}{2}\Delta \text{BIC}_r\right)}, \tag{6}$$

where g_i is the model, ΔBIC_i is the difference between the BIC of model g_i and the minimum BIC value among the set of models, and R represents the set of models. We follow the rule of thumb proposed by Raftery (1995, Table 6) to interpret posterior probabilities. According to this author, the evidence for supporting model g_i over the others is weak if posterior probabilities are smaller than 0.75, positive if they lie between 0.75 and 0.95, strong if they lie between 0.95 and 0.99, and very strong if they are larger than 0.99.

In addition, we assessed the models' robustness by evaluating their ability to predict the actual altitudinal limits of the species. While we are aware that species may not be at equilibrium with the environment and have probably not yet filled their potential range, the current altitudinal limits of the species are probably close to equilibrium with climate and might be explained by survival probability because of major thermal-related physiological constraints (Dangles et al., 2008). We calculated with the three models the probability of survival of each species in 50 field sites where moth abundance has been regularly monitored by our team between 2006 and 2008. The probability of survival of each life stage of each species at each site was calculated using WorldClim mean yearly temperature and the 'Map Algebra' tool from ArcMap. The decision to use mean yearly temperatures (as opposed to minimum or maximum temperatures) was based on the strong correlation found between mean temperature and elevation in the Ecuadorian Andes (Dangles et al., 2008). Minimum and maximum temperatures in the tropics are punctual events, both in space and in time (e.g. low early morning temperatures associated with freeze in some valleys), that show poor correlation with altitude (Dangles et al., 2008 and see Appendix B in that same paper). We therefore considered that mean temperature was the best surrogate to investigate altitude-related physiological limitations of our insects. To obtain total survival of each species, we multiplied survival rates of eggs, larvae, and pupae. We then adjusted linear models to the relationships between survival probability and altitude. Finally, predicted survival probabilities along the altitudinal gradient were compared to the observed altitudinal limits and observed abundance of the three species (Dangles et al., 2008).

Results

Model performance

The BIC shows that Régnière's model is most often the one that best explains the data relative to its number of parameters (table 2). Calculations of posterior probabilities show that in four cases (P. operculella's larvae and pupae, S. tangolias' eggs, and T. solanivora's larvae) the evidence for supporting Régnière's model over the others is either strong or very strong. Only in one case (S. tangolias' pupae) there is positive evidence for supporting Sporleder's model over the other two. In all other cases, there is weak evidence supporting any of the three models. Fig. 2 shows the curves generated by the three models for the three stages of the three species. This figure shows how the three models differ mainly in their predictions of survival at extremely high and low temperatures. Parameter values for the three models can be found in Appendix 2.

Model robustness

Simulations with the models using the mean annual temperature of the 50 monitoring sites allowed us to obtain

Table 2. Performance of the three models fitted to survival data of eggs, larvae, and pupae of the three species of PTM. *LL*, log-likelihood; *k*, number of parameters; *n*, number of data; BIC, Bayesian Information Criterion; *P*, posterior probability. Lowest BIC values are in bold font. Bold font in *P* values indicates strong or very strong support for one model over the others.

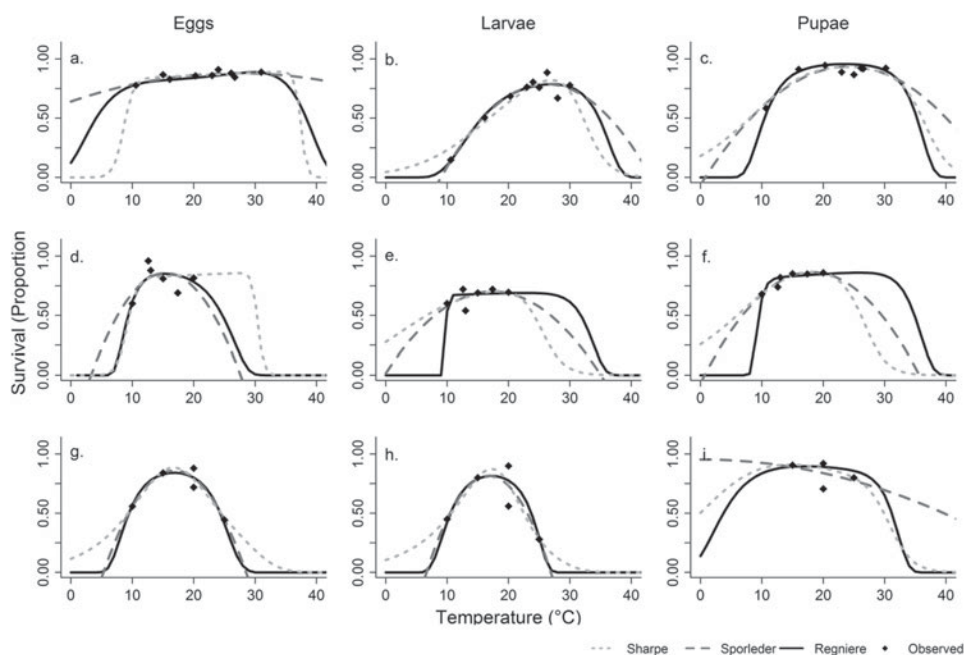|	Eggs			Larvae			Pupae		
	Sharpe	Sporleder	Regniere	Sharpe	Sporleder	Regniere	Sharpe	Sporleder	Regniere
P. operculella									
LL	35.904	37.152	38.150	60.864	40.489	36.450	30.249	32.593	26.771
K	6	3	3	6	3	3	5	3	3
N	9	9	9	9	9	9	8	8	8
BIC	84.99	**80.90**	82.89	134.91	87.57	**79.49**	70.90	71.42	**60.04**
P	0.086	0.667	0.247	<0.001	0.017	**0.983**	0.004	0.003	**0.992**
S. tangolias									
LL	31.978	37.474	22.550	18.937	19.221	20.100	14.122	14.104	18.700
K	5	3	3	5	3	2	5	3	2
N	6	6	6	6	6	6	6	6	6
BIC	72.92	80.32	**50.48**	46.83	43.82	**43.78**	37.20	**33.58**	40.98
P	<0.001	<0.001	**0.999**	0.099	0.446	0.455	0.138	0.841	0.021
T. solanivora									
LL	19.516	19.096	18.450	30.623	30.789	20.550	11.433	12.732	14.147
K	4	3	3	4	3	3	3	2	3
N	5	5	5	5	5	5	4	4	4
BIC	45.47	43.02	**41.73**	67.68	66.41	**45.93**	**27.03**	28.24	32.45
P	0.092	0.313	0.596	<0.001	<0.001	**0.999**	0.620	0.339	0.041

Fig. 2. Survival probability in relation to temperature of eggs, larvae, and pupae of *P. operculella* (a, b, c), *S. tangolias* (d, e, f), and *T. solanivora* (g, h, i). Bullets represent observed survival and lines predicted survival by the three models.

a relationship between predicted survival probability and altitude (fig. 3). For *P. operculella* this relationship is best described by a linear model ($s = ax + b$, with *S* representing survival probability and *x* altitude in m.a.s.l., and $R^2 = 0.57$, 0.56, and 0.55 for predictions by Sharpe and DeMichele's, Sporleder's, and Régnière's models, respectively). *S. tangolias'* survival probability is best described by a cubic model of altitude ($s = ax^3 + b$, R^2 of 0.57, 0.61, and 0.53 for Sharpe and DeMichele's, Sporleder's, and Régnière's models,

respectively). *T. solanivora*'s survival probability is best described by a second-order polynomial of altitude ($s = ax^2 + bx + c$, $R^2 = 0.56$, 0.56, and 0.59 for Sharpe and DeMichele's, Sporleder's, and Régnière's models, respectively). Using these relationships, we assessed the models' ability to predict actual moth high altitude limits. For *P. operculella* and *T. solanivora*, the three models predict moth survival at higher altitudes than the maximum one where moths have ever been observed so far (i.e. 3350 and
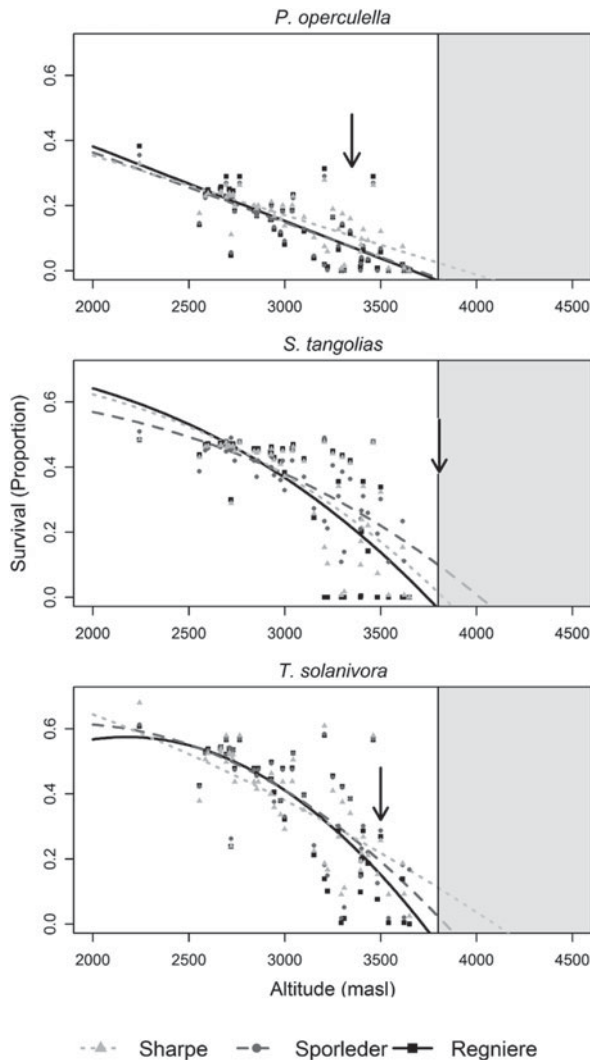
Fig. 3. Predicted survival rates (bullets) of *P. operculella*, *S. tangolias*, and *T. solanivora* by the three models in 50 sites located along an altitudinal gradient in the Ecuadorian Andes. Predicted survival of *P. operculella*, *S. tangolias*, and *T. solanivora* were adjusted to linear, cubic, and second-order polynomial models, respectively. Adjusted models are represented by lines. The gray area symbolizes altitudes above the agricultural frontier, where no crop is cultivated (Gondard & Mazurek, 2001; Liger, 2010), and arrows represent maximum altitudes where moths have been recorded during field monitoring in Ecuador (Dangles et al., 2008).

3500 m.a.s.l., respectively). Sharpe & DeMichele's model greatly overestimates this limit (predicting survival of the two species at altitudes higher than 4000 m.a.s.l.), while the altitudinal limits predicted by the other two are closer to the observed limits. In the case of *S. tangolias*, Régnière's model is the only one that accurately predicts the observed altitudinal limit of the species. It is important to note that these altitudinal limits are valid for the Ecuadorian Andes and that moth altitudinal distribution in other places (i.e. Peru or Bolivia) may differ due to different climatic conditions in such places or to local adaptations of insects. No correlation is found

between moth's predicted survival and observed abundance (Appendix 3). Neither a logarithmic nor a polynomial model fit significantly to the data (R^2 values ranged between 0.21 and 0.39).

Discussion

Comparing various models of insect survival

Accurately predicting the level of success of an invasive insect species in a particular territory necessitates a good description of its climatic niche (Sinclair et al., 2003; Logan et al., 2007). Temperature-related survival constitutes a direct measurement of organisms' tolerance and is an essential component of fitness (Gilchrist, 1995; Angilletta, 2009). Several studies have investigated the influence of temperature on insect survival (Ma, 1997; Perez-Mendoza et al., 2004; Bonato et al., 2007), but this temperature response has rarely been incorporated in predictive phenological models for insects (Bentz et al., 1991; Gilbert et al., 2004; Ma & Bechinski, 2008). Nevertheless, survival responses to temperature have been found to differ from developmental responses, especially in relation to optimum and extreme temperatures (Ma, 1997; Perez-Mendoza et al., 2004; Bonato et al., 2007). In particular, in places where temperatures approach lethal extremes, a precise assessment of physiological limits is important for accurately predicting the risk posed by invasive pests (Régnière et al., 2012). In the specific case of the Ecuadorian Andes, mean temperatures at high altitudes may be frequently close to the lower threshold temperatures for survival, and species' distribution is restricted to altitudes with suitable temperatures (Dangles et al., 2008).

In this study, we compared the ability of three different models to predict temperature-related PTM survival. We were particularly interested in assessing the behavior of these models when fitted with a small dataset that did not cover the whole possible temperature range. Small datasets are indeed a common caveat for many agricultural pests in the tropics, thereby impeding sound predictions of insect survival at temperature extremes (Niño, 2004; Sporleder et al., 2004; Jaramillo et al., 2009). Even though our analyses of posterior probabilities with the BICs showed that in most cases there was weak evidence for supporting one model over the other two, a qualitative assessment of different response curves showed that their predictions differed mostly at temperature extremes. In particular, Régnière's model consistently produced bell-shaped curves with close to 0% survival at low and high temperatures, whereas in two cases (*P. operculella* eggs and *T. solanivora* pupae) Sporleder's polynomial model was unable to produce bell-shaped curves and predicted high survival all along the temperature range. The ability of Régnière's model to produce bell-shaped curves allowed a better estimation of the observed altitudinal limits of the species. Nevertheless, the three models predicted survival of *P. operculella* and *T. solanivora* to altitudes higher than the maximum altitudes where moths have been found during field monitoring in Ecuador (Dangles et al., 2008). The same was observed for predictions of *S. tangolias* survival by Sporleder's and Sharpe & DeMichele's models. This could mean that the actual upper range distribution of these species may not be limited by low temperatures but by other factors such as biotic interactions (competition and predation) or by the agricultural line which corresponds to the potato crop line (Gondard & Mazurek, 2001; Liger, 2010). This suggests that

future lines of research should assess the actual factors limiting the altitudinal distribution of these species in a better manner.

Potential applications

Accurate measures of temperature tolerance are crucial for predicting the consequences of global climate change on pests' fitness and distributions (Deutsch *et al.*, 2008; Jaramillo *et al.*, 2009). Based on simulations of warming tolerance of the Coffee Berry Borer, *Hypothenemus hampei*, Jaramillo *et al.* (2009) predicted devastating effects of global warming on future coffee production. Survival models are useful for evaluating the risk posed by pest species to farmers' crop and agricultural products (Tang *et al.*, 2008). Agricultural landscapes in tropical countries are highly threatened by an increasing number of pest species, but studies are scarce and data are difficult to obtain. We hence believe that the value of Régnière's model lies in its ability to simulate more accurately PTM survival at low and high temperatures when fitted to very few data. This may be particularly useful for models that include insect dynamics under extreme temperature conditions. For example, simulating natural, long-distance dispersal events – during which, insects may be exposed to extremely low atmospheric temperatures (Isard *et al.*, 2005) – requires accurate understanding of the effects of extreme conditions on insect survival. Survival models, as the one proposed in this study, could thus improve our ability to simulate such dispersal events and the actual threats posed by invasive pests.

Predictions of insects population dynamics with models running at fluctuating temperatures have been found to produce more realistic results than with constant temperatures (Gilbert *et al.*, 2004). In a further step, it would thus be interesting to run the survival models under fluctuating daily temperatures, rather than constant annual means. We could expect that the ability of Régnière's model to more accurately predict low temperature mortality will make it more precise when working with temperatures that frequently approach low, lethal temperatures.

The supplementary material for this article can be found at http://www.journals.cambridge.org/BER.

References

Angilletta, M.J. (2009) *Thermal Adaptation: A Theoretical and Empirical Synthesis*. New York, Oxford University Press Inc.

Bentz, B.J., Logan, J.A. & Amman, G.D. (1991) Temperature-dependent development of the mountain pine-beetle (Coleoptera, Scolytidae) and simulation of its phenology. *Canadian Entomologist* **123**, 1083–1094.

Bonato, O., Lurette, A., Vidal, C. & Fargues, J. (2007) Modelling temperature-dependent bionomics of *Bemisia tabaci* (Q-biotype). *Physiological Entomology* **32**, 50–55.

Burnham, K.P. & Anderson, D.R. (2004) Multimodel inference – understanding AIC and BIC in model selection. *Sociological Methods and Research* **33**, 261–304.

Dangles, O., Carpio, C., Barragan, A.R., Zeddam, J.L. & Silvain, J.F. (2008) Temperature as a key driver of ecological sorting among invasive pest species in the tropical Andes. *Ecological Applications* **18**, 1795–1809.

Dangles, O., Carpio, C., Villares, M., Yumisaca, F., Liger, B., Rebaudo, F. & Silvain, J.F. (2010) Community-based participatory research helps farmers and scientists to manage invasive pests in the Ecuadorian Andes. *AMBIO* **39**, 325–335.

Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C. & Martin, P.R. (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the USA* **105**, 6668–6672.

Duyck, P.F., David, P. & Quilici, S. (2006) Climatic niche partitioning following successive invasions by fruit flies in La Reunion. *Journal of Animal Ecology* **75**, 518–526.

Geurts, K., Mwatawala, M. & De Meyer, M. (2012) Indigenous and invasive fruit fly diversity along an altitudinal transect in Eastern Central Tanzania. *Journal of Insect Science* **12**, 1–18. Available online: insectscience.org/12.12.

Gilbert, E., Powell, J.A., Logan, J.A. & Bentz, B.J. (2004) Comparison of three models predicting developmental milestones given environmental and individual variation. *Bulletin of Mathematical Biology* **66**, 1821–1850.

Gilchrist, G.W. (1995) Specialists and generalists in changing environments 0.1. Fitness landscapes of thermal sensitivity. *American Naturalist* **146**, 252–270.

Gondard, P. & Mazurek, H. (2001) 30 años de reforma agraria y colonización en el Ecuador (1964–1994): dinámicas espaciales. pp. 15–40 *in* Gondard, P. & León, J.B. (*Eds*) *Dinámicas Territoriales: Ecuador, Bolivia, Perú, Venezuela*. Quito, Estudio de Geografía.

Hodkinson, I.D. (2005) Terrestrial insects along elevation gradients: species and community responses to altitude. *Biological Reviews* **80**, 489–513.

Isard, S.A., Gage, S.H., Comtois, P. & Russo, J.M. (2005) Principles of the atmospheric pathway for invasive species applied to soybean rust. *Bioscience* **55**, 851–861.

Jaramillo, J., Chabi-Olaye, A., Kamonjo, C., Jaramillo, A., Vega, F.E., Poehling, H.M. & Borgemeister, C. (2009) Thermal tolerance of the coffee berry borer *Hypothenemus hampei*: predictions of climate change impact on a tropical insect pest. *PLoS ONE* **4**, e6487.

Liger, B. (2010) Elaboración de Mapas predictivos de riesgo de infestación de tres especies de polillas de la papa (Lepidoptera: Gelechiidae). Licenciatura dissertation, PUCE, Quito.

Logan, J.A., Régnière, J., Gray, D.R. & Munson, A.S. (2007) Risk assessment in the face of a changing environment: gypsy moth and climate change in Utah. *Ecological Applications* **17**, 101–117.

Luo, Y.Q., Ogle, K., Tucker, C., Fei, S.F., Gao, C., LaDeau, S., Clark, J.S. & Schimel, D.S. (2011) Ecological forecasting and data assimilation in a data-rich era. *Ecological Applications* **21**, 1429–1442.

Ma, Z.S. (1997) Demography and survival analysis of Russian wheat aphid populations. PhD dissertation, University of Idaho.

Ma, Z.S. & Bechinski, E.J. (2008) Developmental and phenological modeling of Russian wheat aphid (Hemiptera: Aphididae). *Annals of the Entomological Society of America* **101**, 351–361.

Niño, L. (2004) Revisión sobre la Polilla de la Papa *Tecia solanivora* en Centro y Suramérica. *Suplemento Revista Latinoamericana de la Papa* 18 pp.

Nyssen, J., Poesen, J. & Deckers, J. (2009) Land degradation and soil and water conservation in tropical highlands. *Soil and Tillage Research* **103**, 197–202.

Palacios, M., Tenorio, J., Vera, M., Zevallos, F. & Lagnaoui, A. (1998) Population dynamics of the Andean potato tuber moth, *Symmetrischema tangolias* (Gyen), in three different agro-ecosystems in Peru. *CIP – Program Report* 153–160.

Perez, C., Nicklin, C., Dangles, O., Vanek, S., Sherwood, S., Halloy, S., Martinez, R., Garret, K. & Forbes, G. (2010) Climate change in the high Andes: implications and adaptation strategies for small scale farmers. *International Journal of Environmental, Cultural, Economic and Social Sustainability* **6**, 78–88.

Perez-Mendoza, J., Weaver, D.K. & Throne, J.E. (2004) Development and survivorship of immature Angoumois grain moth (Lepidoptera : Gelechiidae) on stored corn. *Environmental Entomology* **33**, 807–814.

Raftery, A.E. (1995) Bayesian model selection in social research. *Sociological Methodology* **25**, 111–163.

Rebaudo, F., Dangles, O., Lery, X., Lopez-Ferber, M. & Zeddam, J.L. (2006) Biological efficacy of a granulovirus for the control of *Tecia solanivora*, Povolny (1973). pp. 826–834 *in* Proceedings of the 8th International Conference on Plant Diseases (Tours, France, 5–6 December, 2006). Alfortville, France, Association Française de Protection des Plantes.

Régnière, J., Powell, J., Bentz, B. & Nealis, V. (2012) Effects of temperature on development, survival and reproduction of insects: experimental design, data analysis and modeling. *Journal of Insect Physiology* **58**, 634–647.

Roux, O. (1993) *Population Ecology of Potato Tuber Moth Phthorimaea operculella (Zeller) (Lepidoptera:Gelechiidae) and Design of an Integrated Pest Management Program in Tunisia*. Zurich, Doctor of Technical Sciences. Swiss Federal Institute of Technology.

Schoolfield, R.M., Sharpe, P.J.H. & Magnuson, C.E. (1981) Non-linear regression of biological temperature-dependent rate models based on absolute reaction-rate theory. *Journal of Theoretical Biology* **88**, 719–731.

Schwarz, G. (1978) Estimating dimension of a model. *Annals of Statistics* **6**, 461–464.

Sharpe, P.J.H. & DeMichele, D.W. (1977) Reaction-kinetics of poikilotherm development. *Journal of Theoretical Biology* **64**, 649–670.

Sinclair, B.J., Vernon, P., Jaco Klok, C. & Chown, S.L. (2003) Insects at low temperatures: an ecological perspective. *Trends in Ecology & Evolution* **18**, 257–262.

Sporleder, M., Kroschel, J., Quispe, M.R.G. & Lagnaoui, A. (2004) A temperature-based simulation model for the potato tuberworm, *Phthorimaea operculella* Zeller (Lepidoptera; gelechiidae). *Environmental Entomology* **33**, 477–486.

Sporleder, M., Kroschel, J., Huber, J. & Lagnaoui, A. (2005) An improved method to determine the biological activity (LC50) of the granulovirus PoGV in its host *Phthorimaea operculella*. *Entomologia Experimentalis et Applicata* **116**, 191–197.

Tang, P.A., Wang, J.J., He, Y., Jiang, H.B. & Wang, Z.Y. (2008) Development, survival, and reproduction of the psocid *Liposcelis decolor* (Psocoptera: Liposcelididae) at constant temperatures. *Annals of the Entomological Society of America* **101**, 1017–1025.

Torres, W., Notz, A. & Valencia, L. (1997) Cliclo de vida y otros aspectos de la biologia de la polilla de la papa *Tecia solanivora* (Povolny) (Lepidoptera: Gelechiidae) en el estado Tachira, Venezuela. *Boletín de Entomología Venezolana* **12**, 81–94.

van der Have, T.M. (2002) A proximate model for thermal tolerance in ectotherms. *Oikos* **98**, 141–155.

Young, K.R. (2009) Andean land use and biodiversity: humanized landscapes in a time of change. *Annals of the Missouri Botanical Garden* **96**, 492–507.