

Changes in the distribution of multispecies pest assemblages affect levels of crop damage in warming tropical Andes

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Abstract

Climate induced species range shifts might create novel interactions among species that may outweigh direct climatic effects. In an agricultural context, climate change might alter the intensity of competition or facilitation interactions among pests with, potentially, negative consequences on the levels of damage to crop. This could threaten the productivity of agricultural systems and have negative impacts on food security, but has yet been poorly considered in studies. In this contribution, we constructed and evaluated process-based species distribution models for three invasive potato pests in the Tropical Andean Region. These three species have been found to co-occur and interact within the same potato tuber, causing different levels of damage to crop. Our models allowed us to predict the current and future distribution of the species and therefore, to assess how damage to crop might change in the future due to novel interactions. In general, our study revealed the main challenges related to distribution modeling of invasive pests in highly heterogeneous regions. It yielded different results for the three species, both in terms of accuracy and distribution, with one species surviving best at lower altitudes and the other two performing better at higher altitudes. As to future distributions our results suggested that the three species will show different responses to climate change, with one of them expanding to higher altitudes, another contracting its range and the other shifting its distribution to higher altitudes. These changes will result in novel areas of co-occurrence and hence, interactions of the pests, which will cause different levels of damage to crop. Combining population dynamics and species distribution models that incorporate interspecific trade-off relationships in different environments revealed a powerful approach to provide predictions about the response of an assemblage of interacting species to future environmental changes and their impact on process rates.

Keywords: agricultural pests, climate change, climatic variability, hazard mapping, heterogeneous landscapes, individual based model, *Phthorimaea operculella*, potato tuber moth, *Symmetrischema tangolias*, *Tecia solanivora*

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Introduction

Evidence of global warming continues to mount and according to general circulation models temperature rise will persist in the future (IPCC, 2013). Current climate change is predicted to affect species' distribution and population density (Parmesan, 2006). However, such direct consequences might be outweighed or even reversed by indirect effects of climate change, through its effects on the type, frequency, and intensity of biotic interactions (Tylianakis *et al.*, 2008; Angert *et al.*, 2013; Blois *et al.*, 2013; Buckley, 2013). The actual outcomes of

climate change on community structure and on ecosystem functions may thus be better understood if biotic interactions are considered (Bellard *et al.*, 2012; Blois *et al.*, 2013). Including more than one species and biotic interactions in models may improve their performance and may provide with more realistic predictions on the actual effects of climate change (Hof *et al.*, 2012; Blois *et al.*, 2013). Moreover, efforts should be made to incorporate into model predictions the consequences of changing interspecific interactions on ecosystem functioning (Bellard *et al.*, 2012). Nevertheless, with the exception of plant-pollinator relationships (Klein *et al.*, 2007; Potts *et al.*, 2010; Garibaldi *et al.*, 2013; Vieira *et al.*, 2013), this issue has been to date, poorly considered.

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A major threat of climate change on global food security concerns the effects of warming temperatures on pests and diseases (Chakraborty & Newton, 2011). Although interactions between climate change, crops and pests are complex, a recent study has shown that crop pests and pathogens have altered their latitudinal ranges in response to global warming (Bebber *et al.*, 2013). Climate change might alter the vulnerability of certain regions to pest by producing new areas of pest co-occurrence where these might interact, either positively (facilitation) or negatively (competition), thus altering the levels of damage to crop (Dangles *et al.*, 2013a). This could threaten the productivity of agricultural systems and have negative impacts on food security, especially in areas currently vulnerable to hunger and under nutrition, like the tropical Andes (Perez *et al.*, 2010; Wheeler & Von Braun, 2013). Predictions on pests' distribution, interspecific interaction strength, and impacts on crop losses under current and future climate are therefore crucial and timely since they can provide stakeholders with decision making tools to anticipate risks to crop. However, we are not aware of any predictive model that relates the level of crop damage resulting from changes in biotic interactions caused by climate induced range shifts.

Here, we describe and evaluate process-based species distribution models for three interacting, invasive Potato Tuber Moth (PTM, Lepidoptera: Gelechiidae) in the highly heterogeneous Tropical Andean Region. High-altitude tropical regions are predicted to be more strongly affected by climate change than their surrounding lowlands, due to decreasing lapse rate (Bradley *et al.*, 2006; Buytaert *et al.*, 2010), but predicting distributions in such highly heterogeneous regions is a challenging task and it may be difficult to obtain accurate and realistic predictions. Three species of PTM, *Phthorimaea operculella* (Zeller), *Symmetrischema tangolias* (Gyen), and *Tecia solanivora* (Povolny), have been invading agricultural landscapes of the region within the last 30 years and cause considerable losses in yield in the potato fields of the North Andes, especially in the poorest regions (Dangles *et al.*, 2008). They have been found to sometimes co-occur and interact (either positively or negatively) causing varying levels of damage to crop, depending on temperature, the sequence of arrival to the tuber and the level of biotic stress (i.e. tuber resistance) (Mazoyer, 2007; Dangles *et al.*, 2013a,b). This study aimed at predicting the future distribution of the three interacting species, and therefore to assess how damage to crop might change in the future due to novel interactions.

Materials and methods

Study region

Our study concerned the Tropical Andes, located in North-West South America between the latitudes of approximately 10°N and 20°S and in the countries of Colombia, Ecuador, Peru, and Bolivia. We focused our study on areas above 1000 m.a.s.l. because potato is only cultivated above this altitude (except in a few coastal areas in Peru). The total area considered spanned 2 033 000 km². One of the most prominent features of the study region is its high spatial heterogeneity, mainly related to changes in elevation (Young & Lipton, 2006; Young, 2009). The region also lacks a marked seasonality in temperature (Dangles *et al.*, 2008), but as latitude increases, temperature seasonality becomes more apparent. The Tropical Andes nevertheless, present temporal variability in precipitation which is however complex and difficult to predict because precipitation regime is influenced by El Niño Southern Oscillation (ENSO) (Young, 2009; Poveda *et al.*, 2011; Williams *et al.*, 2011), the passage of the inter-tropical convergence zone (ITCZ, the area near the equator where winds originating in the northern and southern hemispheres come together), and the influence of moisture-laden winds coming from the Amazon (Poveda *et al.*, 2011).

Potato tuber moth model

We constructed an individual based model that mimicked potato tuber moth (PTM) population dynamics in response to temperature in the tropical Andean Region. This model simulated development, survival and oviposition rate for the three species of PTM based on their stage-specific response functions to temperature. Although we are aware that PTM has been shown to be strongly influenced by precipitation (Foot, 1974; Whiteside, 1980) we excluded precipitation from our model because a cross-correlation analysis between precipitation and PTM abundance in three sites in our study region showed us that this variable has little influence on moth abundance (see Appendix S1 for further details).

Population growth rate. The output of our model was population growth rate, which was calculated at each time step (4 h) as follows:

$$N_{E,t+1} = N_{E,t} S_t(T) + O_{t+1} \quad (1)$$

with N_E the number of eggs at time t , S survival probability as a function of temperature (T) at time t , and O number of eggs laid by females at time $t + 1$.

Daily development rate sub model. Potato tuber moth daily development rate was modeled as a function of temperature with the Sharpe & Demichele (1977) equation as modified by Schoolfield *et al.* (1981):

$$D(T) = \frac{\frac{dT}{298.16} \exp \left[\frac{e}{R} \left(\frac{1}{298.16} - \frac{1}{T} \right) \right]}{1 + \exp \left[\frac{f}{R} \left(\frac{1}{g} - \frac{1}{T} \right) \right] + \exp \left[\frac{h}{R} \left(\frac{1}{i} - \frac{1}{T} \right) \right]} \quad (2)$$

where T is temperature in °Kelvin ($^{\circ}\text{C} + 273.15$), $R = 1.987$, and d, e, f, g, h , and i estimated parameters. In the model, individuals cumulate daily development rates until attaining a value of 1 (time when they change of stage). Thus, development includes either ageing within the same stage or changing to the next one (i.e. from egg to larva, larva to pupa or pupa to adult). Variability in developmental rates (i.e. stochastic variability between individuals due to genetic differences or phenotypic plasticity) was included by assigning each newly created individual a different value of deviation from mean development time for each life stage, according to a lognormal distribution estimated from the experimental data.

Survival probability sub model. Temperature-related survival probability for each stage of each species was calculated with Régnière's model (Régnière *et al.*, 2012; Crespo-Pérez *et al.*, 2013):

$$S(T) = \left(\frac{e^{a+bT+cT^2}}{1 + e^{a+bT+cT^2}} \right)^{D(T)} \quad (3)$$

where a, b , and c are estimated parameters. Individual survival during each time step was simulated by drawing a uniformly-distributed random number ranging from 0 to 1 and removing the individual if this number was larger than the survival probability during that time step.

Oviposition rate sub model. Following Régnière *et al.* (2012) we developed a new formal methodological framework to model temperature dependent oviposition rate of insects. Briefly, Régnière's model acknowledges the diminishing return pattern of cumulative oviposition commonly reported in the literature for a wide variety of insects (e.g., Kim & Lee, 2003, 2010; Kouloussis *et al.*, 2011) and assumes that each unit of time females oviposit a constant proportion, κ (here also termed oviposition decay rate), of their remaining fecundity. Based on this model, the number of eggs laid accumulating from the onset of the oviposition period t_0 to time t , at a specific temperature T , can be calculated as:

$$O_t = F_0 \left[1 - e^{-\kappa(T)(t-t_0)} \right] \quad (4)$$

where F_0 represents temperature related fecundity. Data from several females raised at the same temperature may be fitted to Eqn (5) to account for individual variation in cumulative oviposition:

$$O_{ijk} = \delta_{jk} F_0 [1 - e^{-\kappa(T)(t-t_0)}] \quad (5)$$

δ_{jk} (with mean 1 and variance σ_δ^2) represents the 'lack of fit' between the theoretical oviposition rate at each temperature treatment k and the actual oviposition of each individual j . F_0 , σ_δ , t_0 , and κ may be estimated through maximum likelihood, knowing that the probability of O_{jk} eggs being laid at

temperature T from the onset of oviposition to time t is a log-normal cumulative density function of δ :

$$f(\delta_{jk}) = \frac{1}{\delta \sqrt{2\pi\sigma_\delta^2}} e^{-\frac{y^2}{2\sigma_\delta^2}} \quad (6)$$

where $y = [\ln(\delta_{jk}) + \sigma_\delta^2/2]/\sigma_\delta$. The negative log likelihood to be minimized is:

$$LL = - \sum_j \sum_k \ln[f(\delta)] \quad (7)$$

Usually cumulative oviposition is measured at several constant temperatures. In such cases, cumulative oviposition at each temperature should be modeled separately with Eqn (4) [Eqns (5–7) should be used in cases where data from more than one female exist for each temperature]. This allows one to obtain one value of parameters F_0 , t_0 , and κ for each temperature. The relationship between those parameters and temperature may be evaluated with nonlinear functions. Sporleder *et al.* (2004) approximated the relationship between F_0 and temperature by a second degree polynomial (three parameters). Here, we propose a more flexible parabolic function with four parameters:

$$F_0 = l + mAbs|T - T_0|^x \quad (8)$$

where l, m, T_0 , and x are estimated parameters. The addition of a fourth parameter allows a greater variety of parabolic shapes.

κ from Eqn (4) represents the proportion of eggs out of their remaining fecundity laid by each female at each unit of time, assuming that cumulative oviposition follows a diminishing return pattern. The relationship between κ and temperature was modeled with Sharpe & Demichele (1977) model modified by Schoolfield *et al.* (1981). Since sex ratio of PTM species is close to one (Herrera, 1998; Makee & Saour, 2001) half of the pupae that transformed into adults were considered as ovipositing females. Adult longevity in relation to temperature was also modeled with the modified Sharpe & Demichele (1977) model. In the case of t_0 we assumed no relationship with temperature and thus used mean pre-oviposition period across all temperatures as a single temperature independent constant. However, if a relationship between this variable and temperature is found we propose adjusting it to a nonlinear equation (e.g., Sharpe & Demichele, 1977).

Finally, Eqn (9) may be fitted to the entire dataset:

$$O_t = [l + mAbs|T - T_0|^x] [1 - e^{-\kappa(T)(t-t_0)}] \quad (9)$$

with $t > t_0$.

Potato tuber moth model parameterization

We applied the submodels to lab-derived data of temperature-related development, survival and oviposition, obtained from laboratory experiments performed in the Andean region (Notz, 1995; Torres *et al.*, 1997; Herrera, 1998; Palacios *et al.*, 1998; Alvarez & Trillos, 1999; Sporleder *et al.*, 2004; Castillo, 2005; Dangles *et al.*, 2008) and unpublished data from laboratory experiments that we carried out at the Entomology

Table 1 Values for AUC and one-tailed binomial probability test used to measure the accuracy of our model to simulate PTM distribution. Numbers between parentheses represent *P*-values for the AUC

	AUC	One-tailed binomial test (<i>P</i> -value)
<i>P. operculella</i>	0.44 (0.87)	<0.05
<i>S. tangolias</i>	0.61 (<0.05)	<0.001
<i>T. solanivora</i>	0.86 (<0.001)	<0.001

Laboratory of the Pontifical Catholic University of Ecuador. Data used for development and survival are shown in Table 1 in Crespo-Pérez *et al.* (2013). Oviposition data for *P. operculella* are those from Fig. 6a in Sporleder *et al.* (2004), whereas data for *S. tangolias* and *T. solanivora* are shown in Appendix S2 of this publication.

Parameter values for the three submodels and the three species are shown in Appendix S3. For the development-rate and survival probability submodels, parameters were estimated using log likelihood assuming that development time is near-normally distributed (central limit theorem) and the number of survivors out of the initial number in each treatment is binomially-distributed (see Crespo-Pérez *et al.*, 2013). Diagrams showing the relationship between temperature and development-rate adjusted to the data are presented in Appendix S4. Survival probability curves are shown in Fig. 2 in Crespo-Pérez *et al.* (2013). In the case of oviposition, parameterization differed between *P. operculella* and the other two species. For the first species we used data published by Sporleder *et al.* (2004, their Figure 6a) who measured cumulative oviposition under seven constant temperatures. For *S. tangolias* and *T. solanivora* we used oviposition data from several females raised at 12, 19, and 28 °C in a Memmert climatic chamber (Model HPP 749, Schwabach, Germany) in our lab. We are not aware of any oviposition rate data obtained at fluctuating temperatures for these species (in fact they are nonexistent for many species) although we recognize that further validation of the model with data obtained at fluctuating environments would be a necessary further step for our study (see Gilbert *et al.*, 2004).

We used Eqn (4) to model *P. operculella*'s oviposition rate at each temperature. We fixed F_0 from the experimental data, and estimated the values of κ and t_0 by nonlinear least squares using Microsoft Excel's Solver[®]. In the case of *S. tangolias* and *T. solanivora*, we used Eqns (5–7) to model oviposition rate at each temperature.

For the three species we obtained different values for t_0 , F_0 , and κ , for each temperature. We therefore had seven values for *P. operculella* and three for *S. tangolias* and *T. solanivora* (one value per temperature treatment, see Table 2 in Appendix S3). We then examined the relationship between those parameter values and temperature. We used Eqn (8) to obtain temperature-related fecundity curves (Appendix S4). In the case of *S. tangolias* and *T. solanivora* we fitted this equation to published fecundity data (see Appendices S3 and S4). In the case of κ we used Sharpe & Demichele (1977) model modified by

Schoolfield *et al.* (1981). For *S. tangolias* and *T. solanivora* we varied only parameters d and i because we only had three values for κ (at 12, 19 and 28 °C). The remaining parameters were the same as those fitted for *P. operculella*. Since there was no clear relationship between t_0 and temperature we left it as a single, temperature independent constant which corresponded to the mean pre-oviposition period across all temperatures. Finally, Eqn (9) was fitted to the complete data sets to model cumulative oviposition across all temperatures.

Climate data used for model's simulations

To run our model in the Tropical Andes we used detailed data on topographic variation of the region, and on historical and future weather variation. Topographical data were obtained with Digital Elevation Models (DEM's) of the Tropical Andean Region (Colombia, Ecuador, Peru, and Bolivia) from CGIAR-CSI GeoPortal which provides SRTM 90 m Digital Elevation Data for the entire world (Jarvis *et al.*, 2008). Digital elevation models information was used to interpolate weather station data to the whole region.

Historical weather data were obtained from several sources: (i) Global Summary Of the Day (GSOD) database for the period 1961–2009 found at the National Climate Data Center's (NCDC) site (<ftp.ncdc.noaa.gov/pub/data/g sod/>); (ii) Global Historical Climatology Network (GHCN) data from the National Oceanic and Atmospheric Administration (NOAA); (iii) monthly reports of the period 2000–2006 from the National Meteorology and Hydrology Institute of Ecuador (INAMHI, www.inamhi.gov.ec/anuarios/). GSOD and GHCN data consisted of daily minimum and maximum temperatures and those from INAMHI of mean monthly minimum and maximum temperatures for each year of the period.

Future climate predictions were obtained from the International Centre for Tropical Agriculture's (CIAT) GCM Downscaled Data Portal (http://ccafs-climate.org/download_sres.html). Several GCM models are available at this site. We chose the second generation coupled global climate model (CGCM2) developed by the Canadian Centre for Climate Modelling and Analysis (CCCMA). This is a transient model that considers that if CO₂ levels were held constant at any point in time, temperature would continue to increase until equilibrium was reached. Future projections are available for two IPCC SRES scenarios: A2 and B2. Even though downscaling methods may produce unrealistic results in highly heterogeneous landscapes like the Andes, where topography may cause considerable variations in anomalies, we are not aware at the moment of other climate change data for the region at this resolution.

PTM distribution simulations

Our models were implemented into the BioSIM system (Régnière, 1996) which is an attractive and efficient tool for simulating dynamics at regional scales. BioSIM allowed us to obtain maps of target events such as PTM population survival, mean number of generations and population growth rate in the Tropical Andean Region. The BioSIM system runs the

PTM models for each location sampled from a DEM with a resolution of 30 s (i.e. about 1 km in the Equator). We ran the model at 5000 locations and then interpolated these sampled points to result in a continuous map of target events. Potato cultures are found above 1000 m.a.s.l. in the Andean region (Hijmans, 2001). We used this information to exclude zones below this altitude and thus generate a DEM of potato culture zones of the Tropical Andean Region. The BioSIM modeling process is explained in more detail below.

Climate data interpolation

The first step in the BioSIM system consists in interpolating 30 year normals from the nearest weather stations (GSOD, GHCN, or INAMHI stations) to each sampled location. The interpolation method consists in an inverse distance square weighting technique to correct for differences in elevation, latitude, and longitude between the weather stations and the sampled point (Logan *et al.*, 2007; Régnière *et al.*, 2008). In the case of future climate we calculated the difference between future and current CGCM2 temperature data. This difference was then applied to the weather station historical data to get estimated future temperature at these locations.

Model simulations

We ran the models for ten consecutive years at each of the 5000 locations with the generated weather data. We ran the model with historical weather data (1961–2009) and with climate data of 2020 and 2050 for the two climate change scenarios (A2 and B2). Given the influence of daily variability on insect performance (Worner, 1992; Liu *et al.*, 2002; Meats & Kelly, 2008) we set our model time step to four hours and generated stochastic values of daily minimum and maximum air temperature according to monthly means, variances, and covariance (see Régnière & St-Amant, 2007). This was done both for historical and for future temperature scenarios. We ran five replications for each location and obtained values of mean number of generations per year, mean population growth rate, and mean survival probability for each replication at each location. Since the three types of output presented similar results we will refer only to survival probability in the following. These results were interpolated to the whole region through universal kriging with elevation as external drift (Logan *et al.*, 2007; Régnière *et al.*, 2008). This allowed us to obtain GIS layers of PTM survival probability in the Tropical Andean Region.

Model evaluation

We used observed PTM abundance data from a field survey performed by our team at several sites in Ecuador, Peru, and Bolivia to evaluate the ability of our model to predict moth presence accurately (see Dangles *et al.*, 2008, 2010 for further details on moth monitoring in the region). We evaluated our model's output in several ways:

1. We used the ROC (Receiver Operating Characteristic) curve to assess the ability of our model to predict moth

presence better than random, and calculated the Area Under the ROC curve (AUC) as a measure of model performance (for information regarding the ROC curve see Fielding & Bell, 1997). Since we only disposed of presence data we followed the approach presented in Phillips *et al.* (2006) to build the ROC curve with presence only data, which proposes distinguishing presence from random, rather than presence from absence. For this we randomly chose 5000 background points from the study area and assigned them a value of 0. Pixels that fell in the observed moth presence points (32 points for *P. operculella* and *S. tangolias* and 20 for *T. solanivora*) were assigned a value of 1. Then we used survival probability predicted by our model at each of these points (background and presence points) to construct the ROC curves. We constructed the curves and calculated the AUC with the functions 'roc.plot' and 'roc.area' from the 'verification' library of R (R Core team, 2010). We are aware that ROC curves for species distribution models are normally applied to probability of presence data (Phillips *et al.*, 2006; Morin *et al.*, 2007) and that survival probability is only a surrogate of these. However, we believe that survival probability may be an adequate estimator of our species' presence.

2. We calculated the probability that our model predicted the test localities significantly better than random with a threshold dependent analysis. Following the procedure described by Phillips *et al.* (2006) we first established a threshold to convert survival probability predictions into binary predictions dividing the area into suitable and unsuitable. We chose a different threshold for each species according to the smallest nonzero predicted survival probability value among the test localities at the end of the simulations. Phillips *et al.* (2006) also propose the use of a one-tailed binomial probability test to calculate the probability of having a certain number of successes (presences) out of a given number of trials (test localities) given some probability of success. Probability of success corresponds to the proportion of suitable area for the species with a given threshold. We calculated this probability using Minitab (2009).
3. We compared the spatial patterns of observed adult abundance through time with that of predicted adult abundance after 5 years of simulations at two sites in Ecuador and one in Peru where we surveyed moth abundance from 2006 to 2009. Since we did not have any information about actual initial moth numbers (i.e. at the beginning of the invasion) we were forced to log-transform observed and predicted data to make them comparable.

Moth co-occurrence and interactions

Survival probability, simulated by our model in the 5000 random sites in the Tropical Andes, was transformed into binomial presence-absence predictions, employing the same threshold used for the binomial probability test (see Model evaluation section). This information was then used to calculate the number of locations where only one species was predicted present, two of the species were predicted present or

the three were predicted to co-occur. We are aware that transforming continuous data into binomial presence-absence data may lead to the loss of important information. To understand how this transformation might have impacted our results we quantified the number of cells where one species had very high survival while the other or others had near-threshold survival (5% lower or higher survival than the threshold). Also, we identified the type of interaction (competition or facilitation) occurring in those cells (depending on temperature and species present, see below) to comprehend how these interactions, with one species near-threshold survival, might affect the level of damage to crop.

In addition, a previous study showed that PTM female oviposition may be diminished on tubers that have been previously colonized by a different PTM species (Herrera & Dangles, 2012). This study found that *P. operculella* females oviposit less in tubers previously infested by either *S. tangolias* or *T. solanivora*. *S. tangolias* females oviposit less in tubers previously infested by *T. solanivora*. Whereas females of the latter species are apparently not affected by the other two species and oviposit equally in tubers, independently of previous oviposition by *P. operculella* or *S. tangolias*. To understand how sequence of arrival and preemptive competition might affect moth colonization we first quantified cells that were predicted to be occupied by one or two species in the historic scenario and to harbor additional species in the future scenarios. Then, based on findings by Herrera & Dangles (2012), we quantified in how many of these cells the presence of a species may hamper the arrival of another due to inability to oviposit.

Effect on crop damage

To understand the possible outcomes of interactions on crop damage we used values on crop damage in relation to temperature and species combinations obtained by Dangles *et al.* (2013a). These authors designed an experiment to investigate the influence of temperature on the direction and strength of biotic interactions between PTM, and the related richness effects on crop damage. Their experiment consisted on seven species interaction treatments (three single-species treatments, three two-species treatments, and one three-species treatment) at six different temperatures. They measured tuber mass loss for each treatment and then calculated the mass of consumed potato per unit pupal mass, which they termed tuber processing efficiency (TPE). They also generated expected TPE values for the mixture treatments which corresponded to the average of the TPE of the monocultures for that temperature. At each site of our study we calculated the net effect of moth interaction on crop damage by subtracting expected TPE from observed TPE, depending on mean temperature and species present in that cell. Positive values represented cases of facilitation, negative values represented competition, and null values represented no interaction effect.

Results

Predicted current distribution

Predictions of PTM dynamics in the Tropical Andes (above 1000 m.a.s.l.) showed that *P. operculella* had in

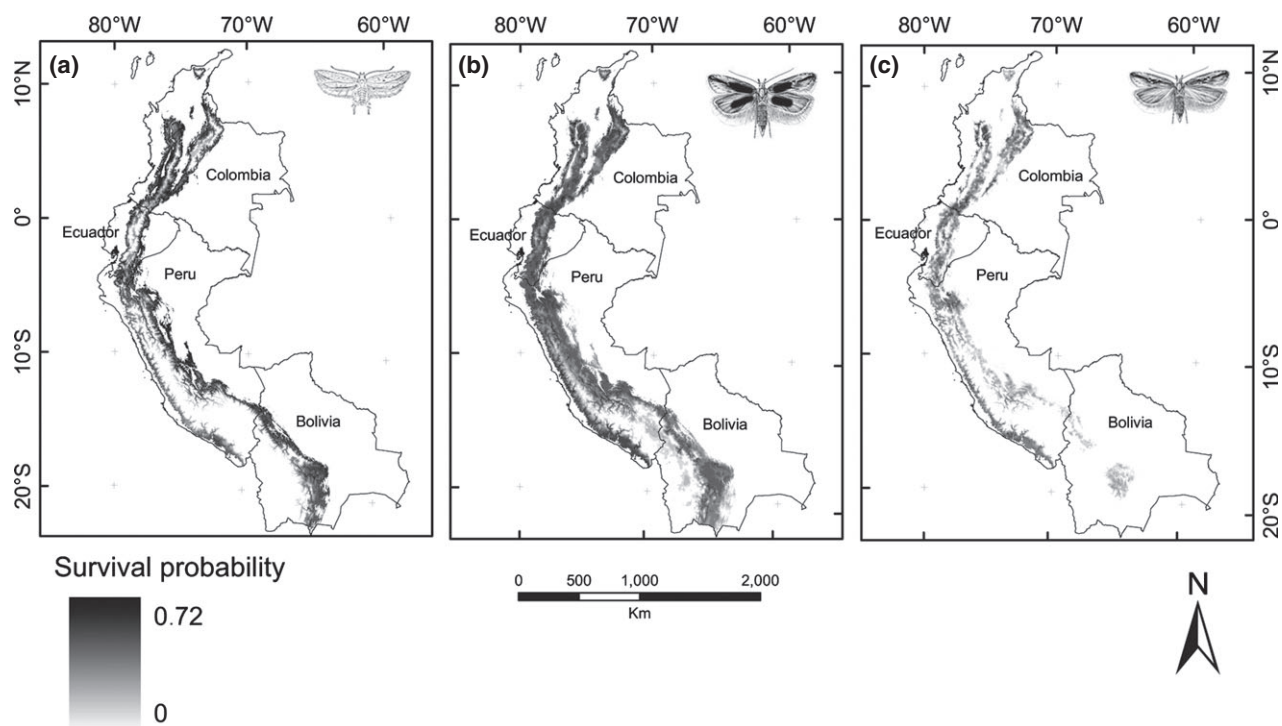


Fig. 1 Maps showing current survival probability predicted by our phenology model for the three species of Potato tuber moth (PTM) in the Northern Andes: (a) *P. operculella*, (b) *S. tangolias*, and (c) *T. solanivora*. Simulations were done only in areas over 1000 m.a.s.l., altitude over which potato is cultivated in the region.

general a higher probability of surviving than the other two species (Fig. 1a). *T. solanivora* showed the lowest overall survival (Fig. 1c) and according to our model none of the species is able to survive in the highest parts of Bolivia (the Altiplano). In general, the three species show higher survival at lower than higher altitudes (Fig. 1).

According to the AUC and Swets (1988) guidelines for interpreting AUC values, our predictions for *P. operculella* and *S. tangolias* are poor but the one-tailed binomial tests showed that the probabilities of our model predicting the localities of observed moth presence are significant for these two species (Table 1, and see Appendix S5 for ROC curves). Our model performs better for *T. solanivora*. AUC values for this species reveal a good prediction and the one-tailed binomial test shows that our model predicts this species' survival in observed localities significantly better than random (Table 1).

Comparing the observed and predicted number of adults at several monitoring sites in the study region shows that in many of the sites where moth presence is constantly observed the model predicts a persistent adult population (Fig. 2). We did not find clear temporal patterns in observed and predicted adult abundance. In some cases we found that our model highly

overestimates adult moth abundance, whereas in other sites our model predicts lower number of adults than those observed during monitoring (Fig. 2). In the case of *P. operculella* our model's predictions are closer to observed adult abundances compared to the two other species (Fig. 2).

Predicted future distribution

The temperature scenarios used for our projections show an increase of 1–3 °C by 2050 in most of the region, with most intensive warming in some parts of Peru and Bolivia (Appendix S6). Only in a few parts of the Eastern Ecuadorian cordillera and the Colombian Andes was the temperature projected to decrease, by 1 °C maximum. According to our model these changes in temperature will change PTM distribution (Fig. 3). Our results show that survival probability will differ among species and between climate change scenarios. As a general trend, the three species tend to increase their distribution range in the future, to a higher level with scenario A2 as compared to B2. Future conditions will apparently be more favorable for *P. operculella* which shows enhanced survival in most of the region. For the other two species conditions seem to be less

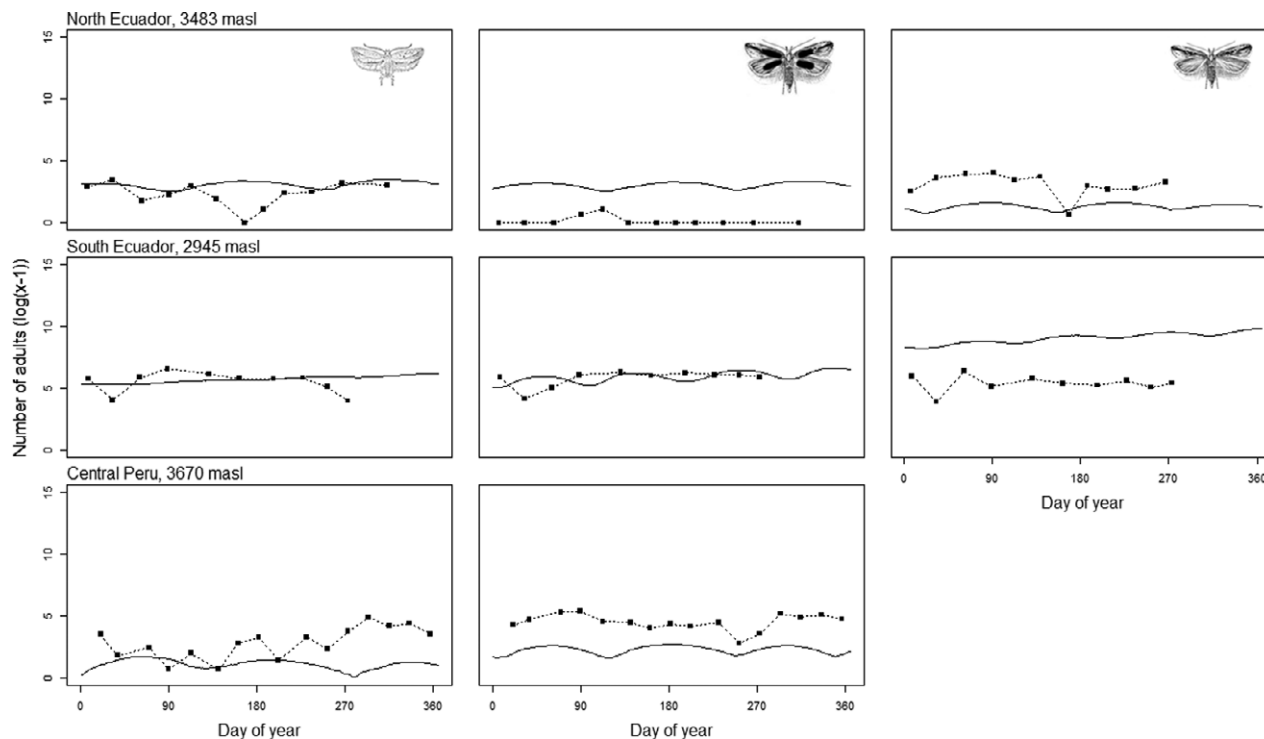


Fig. 2 Observed (dashed line) and predicted (solid line) adult numbers (ln transformed and \log_{10} transformed in the case of observed and predicted numbers respectively) at two sites in Ecuador and one in Peru where a monitoring program has been established. Numbers of predicted adults correspond to numbers for the fifth year of simulation. From left to right: *P. operculella*, *S. tangolias*, and *T. solanivora*.

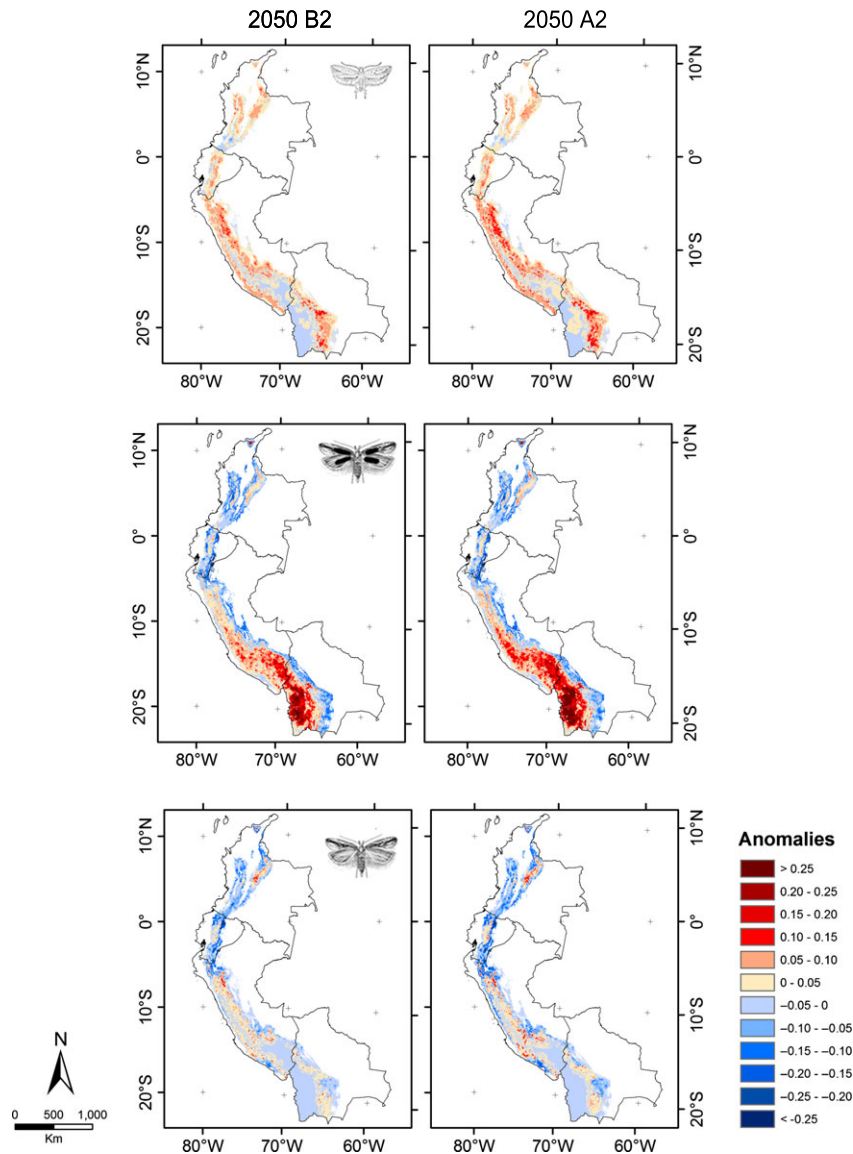


Fig. 3 Predicted future survival probability for *P. operculella* (top panel), *S. tangolias* (center panel), and *T. solanivora* (bottom panel) under the two climate change scenarios, showing the anomalies with respect to current predicted survival.

adequate in many parts of Ecuador and Colombia (Fig. 3).

Influence of altitude and latitude on current and future distribution

To visualize the influence of altitude and latitude on current and future PTM distribution we plotted survival probability against altitude and latitude under current conditions and anomalies in future survival probability for both climate change scenarios (Fig. 4). We found differences in the three species' current distributions with respect to altitude and latitude. For instance, we found that *P. oper-*

cullella is better adapted to lower altitudes (i.e. below 2000 m.a.s.l., Fig. 4a) whereas the other two species seem to perform better at higher altitudes (i.e. *S. tangolias* between 1500 and 3000, Fig. 4b, and *T. solanivora* between 2000 and 3000 m.a.s.l., Fig. 4c). In regards to latitude, the three species perform better close to the equator, with reductions in survival probability towards higher southern latitudes (Fig. 4).

Future climate changes will produce different distributions in the three species through slight changes in survival probability (Fig. 4). Our model suggests that *P. operculella* may expand its distribution due to increased survival probability at altitudes between

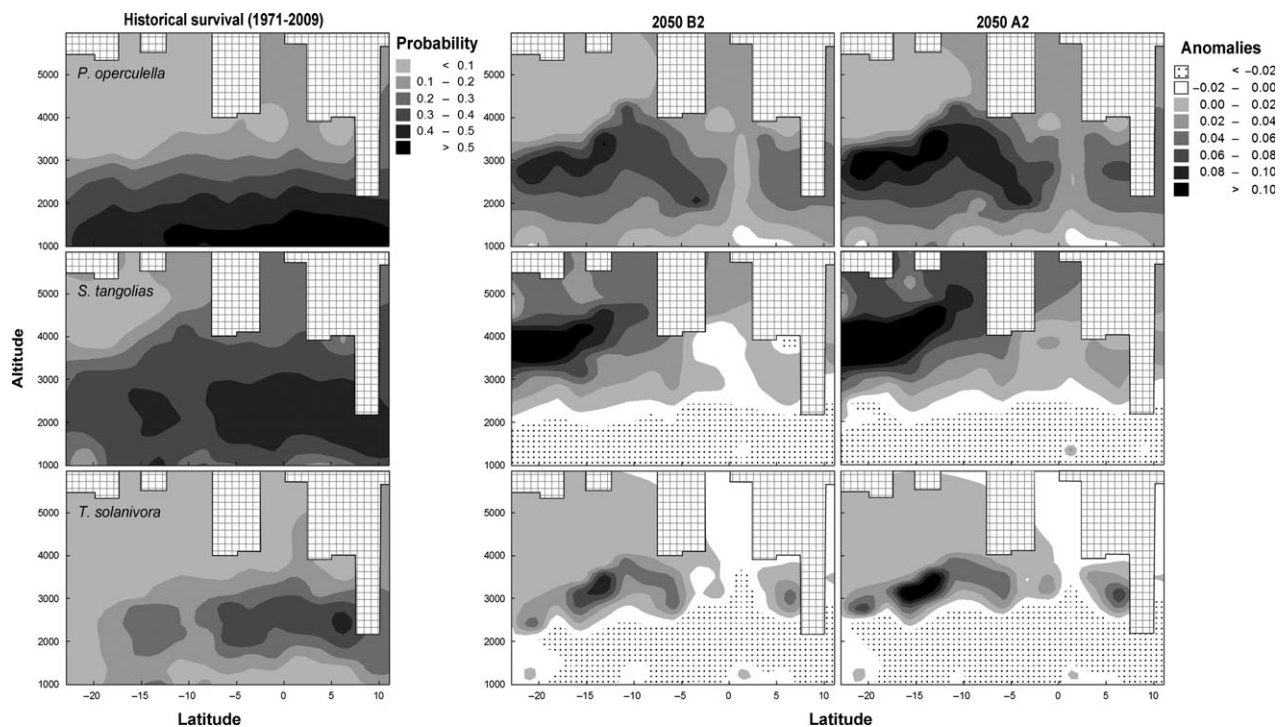


Fig. 4 Contour plots showing the influence of altitude and latitude on present survival probability and future anomalies in survival probability, of the three species of Potato tuber moth (PTM). Areas blocked in tiled texture represent altitudes over which there is no surface (i.e. maximum altitude at each latitude).

c.a. 2500 and 3500 m.a.s.l., and latitudes between c.a. 10 and 25°S. *S. tangolias* may shift its distribution due to increased survival probability at high altitudes (between c.a. 3000 and 4000 m.a.s.l.) and low latitudes (between c.a. 10 and 25°S), and decreased survival at lower altitudes (i.e., below 2000 m.a.s.l.). Finally, according to our results, *T. solanivora*'s distribution will probably contract due to decreased survival probability in most altitudes and latitudes. Only at high altitudes (above 2000) and in latitudes over 5°N and under zero degrees will this species survival probability slightly increase.

Current and future moth co-occurrence and interactions

According to our model, the number of sites free of the pests will decrease and sites with occurrence of only *S. tangolias* and with co-occurrence of this species and *P. operculella* will increase by 2050 (Fig. 5). Our model also suggests that sites with only *P. operculella* will increase by 2050, especially under scenario B2. Contrarily, future climatic conditions might cause the number of places that allow co-occurrence of the three species to decrease. Note that our model suggests that there are currently no sites where *T. solanivora* occurs alone or co-occurs with only *P. operculella*, a pattern that

might remain unchanged in the future. It is important to note that in a very low percentage of cells (5.33%, 6.45%, and 6.36% in the historical, 2050B2 and 2050A2 scenarios respectively) one species occurs at high survival probability while the other or others present near-threshold survival. Most of these cases (c.a. 70%) occur in cells with a temperature and combination of species that favor facilitation rather than competition. Also, our analysis of sequence of arrival showed us that the percentage of cells that are occupied by one or two species in the historic scenario and will harbor additional species in the future is low (7.37% and 8.49% of cells in scenarios 2050 B2 and 2050 A2, respectively, Fig. 6). As previous oviposition by one species in tubers does not necessarily cause another to oviposit less, we found that preemptive competition will only occur in 5% and 6% of cells in scenarios 2050 B2 and 2050 A2 respectively. Those cases occur in cells where only *S. tangolias* or both *S. tangolias* and *T. solanivora* are present in the historic scenario and that allow the presence of *P. operculella* in the future (Fig. 6).

Effect on crop damage

Regarding the impact of moth interactions on crop damage, we found that, currently, positive interactions

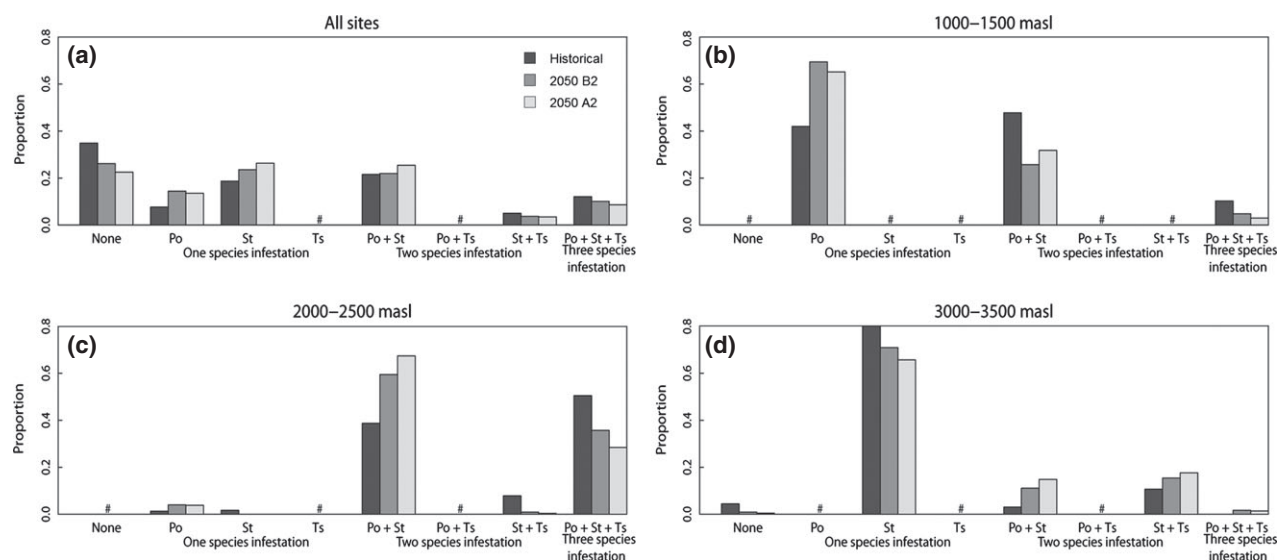


Fig. 5 Proportion of sites where the presence of one of the three species or a combination of two of them or the three of them is predicted by our model under historical climate and two climate change scenarios (2050 B2 and 2050 A2) considering (a) all sites, (b) sites between 1000 and 1500 m.a.s.l., (c) sites between 2000 and 2500 m.a.s.l., and (d) sites between 3000 and 3500 m.a.s.l. # represents cases where zero sites presented a given species combination.

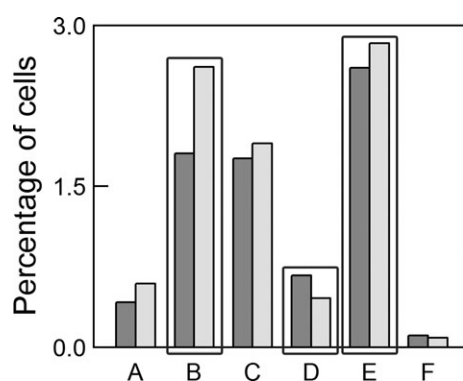


Fig. 6 Percentage of cells with a specific sequence of arrival of Potao tuber moth (PTM) species. (a) Cells that host only *P. operculella* in the current scenario and will allow the additional presence of *S. tangolias* in the future. (b) Cells that host only *S. tangolias* in the current scenario and will allow the additional presence of *P. operculella* in the future. (c) Cells that host only *S. tangolias* in the current scenario and will allow the additional presence of *T. solanivora* in the future. (d) Cells that host only *S. tangolias* in the current scenario and will allow the additional presence of *P. operculella* and *T. solanivora* in the future. (e) Cells that host both *S. tangolias* and *T. solanivora* in the current scenario and will allow the additional presence of *P. operculella* in the future. (f) Cells that host both *P. operculella* and *S. tangolias* in the current scenario and will allow the additional presence of *T. solanivora* in the future. Dark gray = scenario 2050 B2, light gray = scenario 2050 A2. Bars surrounded by gray rectangles represent sequences of arrival where preemptive competition might prevent species from colonizing cells in the future scenarios.

between PTM are mostly important at altitudes between 2000 and 2500 m.a.s.l. (Fig. 7b), with higher values of damage than expected from the added effects of each pest alone. According to our predictions for both climate change scenarios (Fig. 7c, d), facilitation interactions will apparently shift to higher altitudes (i.e. between 2500 and 3000 m.a.s.l.). Note also that in the present interactions above 3000 m.a.s.l. are mostly null (Fig. 7b), but in the future (Fig. 7c, d) we predict an increase of facilitation at such altitudes. It is important to acknowledge that changes in the net effect of interactions on crop damage will not only be due to changes in moth distributions, and assemblages (i.e. cells that host additional or fewer species or different pairs of species in the future scenarios compared to the historic scenario), but also to changes in temperature that may cause shifts in the type of interaction occurring at each cell. Patterns of changes in interaction effect on damage are less clear below 2000 m.a.s.l.

Discussion

Climate change poses serious threats to food security via changes in pests distributions and their establishment in previously unsuitable regions (Bebber *et al.*, 2013). In this contribution we modeled the potential current and future distributions of three important crop pests, and found that not only changes in distribution might pose future threats to crop, but also novel inter-

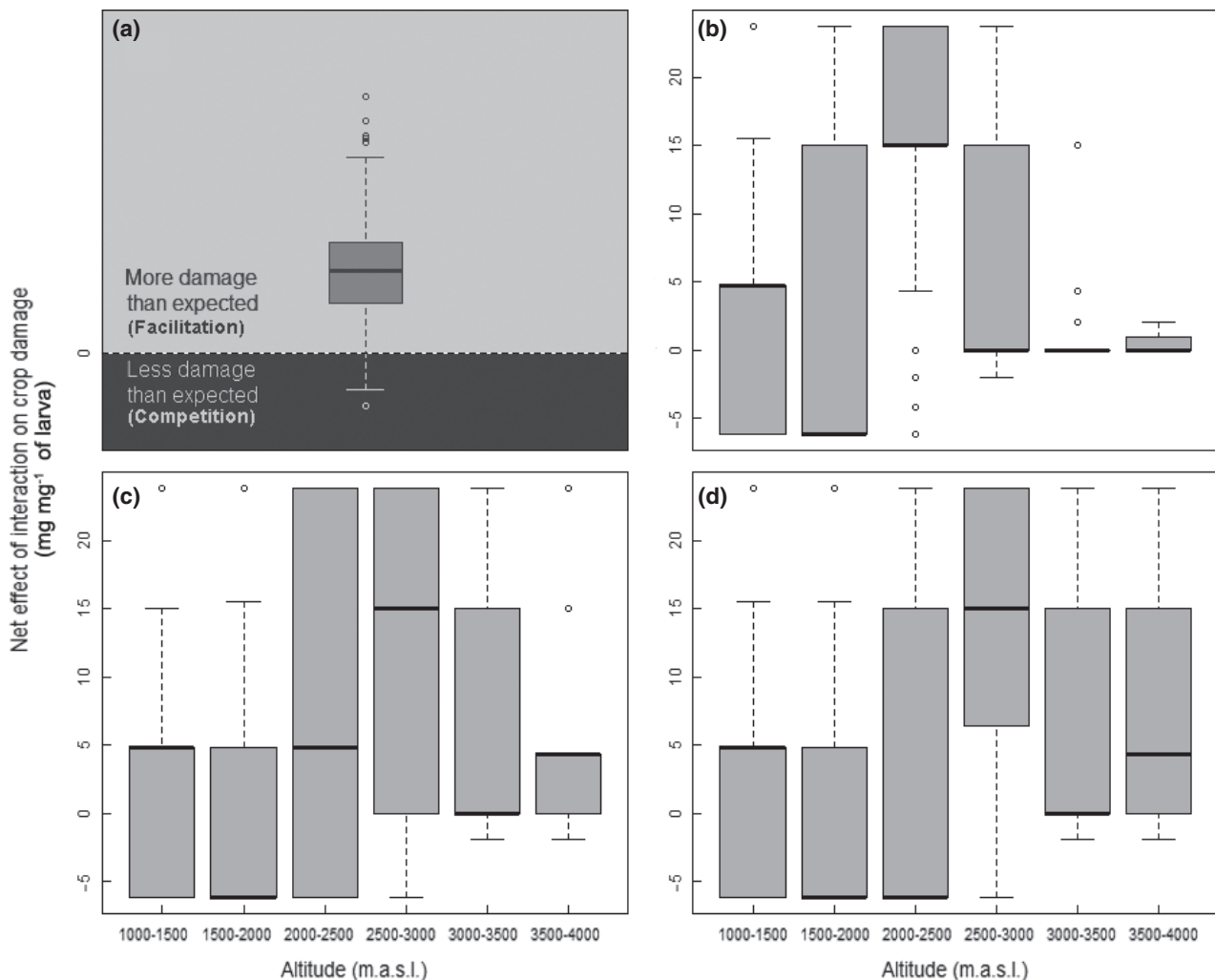


Fig. 7 Boxplots showing the net effect of moth interaction on crop damage. a) Schematic plot showing how to interpret the plots. Values with net effect higher than zero represent cases where damage is higher than that expected from the added effects of each pest alone (facilitation). Values with net effect lower than zero represent cases where damage is lower than that expected from the added effects if each pest alone (competition). (b) Present, (c) 2050 B2 scenario, (d) 2050 A2 scenario.

actions mediated by climate change might shift levels of crop damage.

Building distribution models at regional scales

Ecological models are the most commonly used tool for predicting the effects of climate change on species current and future distribution (Elith & Leathwick, 2009; Sinclair *et al.*, 2010). Distribution models are of particular importance for biosecurity practitioners since they allow the prediction of risk of spread of pest, disease, and weed species (Sutherst, 2014). Among the many existing approaches for modeling pest distribution, process-based models are expected to produce the most robust projections because they are based on causation rather than correlation (Morin *et al.*, 2008). In this

contribution, we investigated the performance of a temperature driven, physiological model for agricultural pests in the Tropical Andes. According to Pearson & Dawson (2003) and Soberon & Peterson (2005), at a coarse scale (regional or continental) climatic influences are dominant and suitable for making predictions about climate change impacts. However, in highly heterogeneous regions, like the Tropical Andes where altitudinal gradients in temperature are often very steep, predictions may be more challenging (Porter *et al.*, 2002; Bonebrake & Deutsch, 2012). We encountered such challenges in this contribution, in which predictions of potential distribution of three closely related pests of the same crop yielded different results in terms of accuracy. We propose four potential explanations for these discrepancies. First, our model did not take into

account the microclimatic heterogeneity that might be influencing pests' dynamics in the Andean mountains. Second, we did not account for human-induced heterogeneity of the region (i.e. distribution of crop storage structures, pesticide application) that may mask or confound the effects of natural drivers of pest invasion and establishment (Crespo-Pérez *et al.*, 2011). Third, the three species considered in this study are invasive species that have recently arrived to many parts of the study region. This means that they have probably not yet reached equilibrium in their distribution. This may be especially true at higher altitudes where, although conditions may be apt for PTM, they may have not yet arrived to those locations (Crespo-Pérez *et al.*, 2013). Fourth, due to the absence of potato cultures above the agricultural frontier the species may be absent from high altitudes due to the absence of their host plant rather than to deleterious temperature conditions. Accounting for all these factors in future modeling approaches of invasive species distributions might be useful for predictions in highly heterogeneous regions. In addition, models like the one presented in this contribution should be considered as predictors of hazard to help managers locate areas vulnerable to pest invasion, rather than predictors of pests' actual distribution.

Altitudinal and latitudinal range shifts

Species respond to climate change by adapting through plasticity and micro-evolution, shifting their distribution or going extinct (Parmesan, 2006; Massot *et al.*, 2008; Robinet & Roques, 2010). Of these responses, distributional shifts have been fairly well documented – especially in species with high dispersal capacities like birds, insects and marine invertebrates (Parmesan, 2006). Distributional changes in altitude and latitude have been observed in more than 1000 species, and include expansions, contractions and range shifts (Bellard *et al.*, 2012). In accordance to Musolin (2007) we found that different responses may occur depending on the species considered. On the one hand, our results suggest that in the future *P. operculella* may expand its range to higher altitudes and lower latitudes as thermal conditions at these locations become suitable, which is in agreement with what has been found for other tropical and subtropical species (Paulson, 2001; Parmesan, 2006; Chen *et al.*, 2009). On the other hand, our results suggest range contraction for *T. solanivora*, and range shift for *S. tangolias* along the altitudinal gradient, which is also in agreement with other studies (Parmesan, 1996; Beever *et al.*, 2003; Wilson *et al.*, 2005).

It is worth noting that although models may predict suitable conditions for species in places outside of their current range, actual range expansion requires that the

species have the sufficient dispersal capabilities to track their climate optimum (Thomas *et al.*, 2004). In the case of our species, and of many species strongly related to human activities like pests, dispersal is frequently associated with movements of humans and their goods (Pitt *et al.*, 2009; Taylor *et al.*, 2012). For instance, Crespo-Pérez *et al.* (2011) showed that the present dispersal speed of *T. solanivora* in central Ecuador is dependent on human-assisted, long-distance dispersal. It is thus likely that the species considered in this study, as well as many agricultural pests, will likely be able to track climate change into suitable areas.

Consequences of interspecific interactions on crop damage

Studies about the influence of climate change on the distribution of PTM and other agricultural pests commonly focus on individual pest species (Juroszek & Von Tiedemann, 2013; Kroschel *et al.*, 2013; Kutywayo *et al.*, 2013; Meynard *et al.*, 2013; Souza *et al.*, 2013). Predictions about the distribution of various related pests are rare (but see Lanteri *et al.*, 2013) and we are not aware of any study that focused on the potential outcomes of pests' co-occurrence and their interactions on crop damage. As stated by Juroszek & Von Tiedemann (2013) interactions are seldom considered in studies relating agricultural pests to climate change. However, as shown by Dangles *et al.* (2013a) pest co-occurrence may produce different levels of damage to crop than that expected from the added effects of each pest alone.

Modeling the distribution of three pests of the same crop allowed us to predict the future areas where two or the three species will co-occur and interact. Also, modeling pest dynamics with climate change scenarios showed that future changes in temperature may alter the types of interactions occurring in the region. These results suggest that future levels of damage to the crop will probably differ from current ones. Moreover, our results revealed a shift of facilitation interactions, to higher altitudes, causing higher levels of damage to crop. This, means that if the raise in altitude of the agricultural frontier continues (Sarmiento, 2002), it may be followed by higher levels of damage at higher altitudes as well. Facilitation interactions may also allow the occurrence of species that alone may not survive. Such is the case of a small percentage of cells in our model where temperature conditions could favor the presence of a species that is at near-threshold survival due to the presence of another species that has very high survival probability, with which it positively interacts. Nevertheless, note that in approximately the same percentage of cells in our model, future colonization of a species may be hampered by previous presence of another, due to preemptive competition, therefore, producing slight

differences in the actual levels of damage predicted in those cells. These two results suggest that the future outcomes of both facilitation and competition interactions should be studied in more depth in future research. In general our results show that combining population dynamics and distribution models that incorporate interspecies trade-off relationships in different thermal environments is a powerful approach to make predictions about the response of an assemblage of interacting species to future environmental changes and their impact on process rates. Our approach is applicable to other pests or species in the same or different regions for which performance rate and environmental data are available. Finally, in the same way that we predict pest co-occurrence, our approach could serve to predict sites of co-occurrence and interaction between predator and prey, host and pathogen or other cases of interspecific interactions.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Influence of precipitation on PTM abundance time series (cross-correlation).

Appendix S2. Daily oviposition data for several females of *S. tangolias* and *T. solanivora* at three constant temperatures (12, 19 and 28 °C).

Appendix S3. Parameter values for the three sub models for the three species of PTM.

Appendix S4. Development rate and total fecundity curves adjusted to published data of PTM dynamics.

Appendix S5. Receiver Operating Characteristic (ROC) curves for current distribution predictions for the three species of PTM in the tropical Andes.

Appendix S6. Present and future mean annual temperatures for two periods in the future, 2020 and 2050, and SRES scenarios B2 and A2.