

Modeling invasive species spread in complex landscapes: the case of potato moth in Ecuador

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Abstract Tropical mountains have a long history of human occupation, and although vulnerable to biological invasions, have received minimal attention in the literature. Understanding invasive pest dynamics in socio-ecological, agricultural landscapes, like the tropical Andes, is a challenging but timely issue for ecologists as it may provide developing countries with new tools to face increasing threats posed by these organisms. In this work, road rehabilitation into a remote valley of the Ecuadorian Andes constituted a natural experiment to study the spatial propagation of an invasive potato tuber moth into a previously non-

infested agricultural landscape. We used a cellular automaton to model moth spatio-temporal dynamics. Integrating real-world variables in the model allowed us to examine the relative influence of environmental versus social landscape heterogeneity on moth propagation. We focused on two types of anthropogenic activities: (1) the presence and spatial distribution of traditional crop storage structures that modify local microclimate, and (2) long-distance dispersal (LDD) of moths by human-induced transportation. Data from participatory monitoring of pest invasion into the valley and from a larger-scale field survey on the Ecuadorian Andes allowed us to validate our model against actual presence/absence records. Our simulations revealed that high density and a clumped distribution of storage structures had a positive effect on moth invasion by modifying the temperature of the landscape, and that passive, LDD enhanced moth invasion. Model validation showed that including human influence produced more precise and realistic simulations. We provide a powerful and widely applicable methodological framework that stresses the crucial importance of integrating the social landscape to develop accurate invasion models of pest dynamics in complex, agricultural systems.

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Introduction

Biological invasion success depends on a sequence of complex interactions between the invader and the recipient ecosystem (Richardson and Pysek 2006). Physical and biological characteristics of landscapes affect their invasibility (i.e. their susceptibility to colonization and establishment of invaders, Davies et al. 2005). Mountain ecosystems are characterized by a high heterogeneity and strong environmental gradients (Körner 2007) that influence the probability of invasion by non-native organisms, especially of ectotherms such as insects (Dangles et al. 2008). High elevation, associated with harsh environmental conditions, high isolation, and low human population densities, makes mountainous environments less susceptible to invasions (MA 2003). However, changes in these patterns, notably due to anthropogenic activities, may reduce mountains' resistance to non-native spread (Pauchard et al. 2009).

Unlike the more pristine temperate mountains, mountains in the tropics are commonly subject to human occupation and disturbance, and are often dominated by land uses associated with agriculture (Nyssen et al. 2009). Although highly vulnerable to invasions, scientific studies on the dynamics of exotic spread in these ecosystems are rare. Most of the literature comes from temperate regions, but patterns observed there can seldom be extrapolated to the tropics where an unmarked seasonality causes daily climate variations to be more important than yearly ones and allows organisms to be active all year round (Dangles et al. 2008). Understanding invasive pest dynamics in these ecosystems is a timely issue for ecologists, as it may provide developing countries with new tools to face increasing threats posed by these organisms. Simulating non-native spread in such heterogeneous environments, while accounting for the influence of anthropogenic activity, is a challenging task which forcefully necessitates a landscape perspective, capable of exploring population dynamics both temporally and spatially (Sebert-Cuvillier et al. 2008).

An increasingly growing range of methodologies are available for describing population spread (for reviews see Hastings et al. 2005 and Jongejans et al. 2008). Spatial structure has been integrated into several types of models, such as patch-based meta-population models (Moilanen 1999; Hanski et al.

2000), stochastic patch occupancy models (SPOMs; Moilanen 2004), individual based models (IBMs; Goslee et al. 2006; Nehrbass et al. 2007; Harris et al. 2009; Carrasco et al. 2010; Travis et al. 2010; Travis et al. 2011), and cellular automata (CA) models (Soons et al. 2005; Herben et al. 2006). An advantage of IBMs and CA is that they may integrate spatial heterogeneity, stochasticity and ecological processes, allowing predictions to be made about the direction and the rate of spread (Jongejans et al. 2008; Cacho et al. 2010).

The general ecological theory behind invasion processes is relatively well understood (Cadotte et al. 2006). Lately there has been great progress in simulating the spatial spread of invasive organisms (Harris et al. 2009; Anderson et al. 2010; Carrasco et al. 2010; Miller and Tenhumberg 2010; Shea et al. 2010; Travis et al. 2011), but several methodological challenges remain to effectively model these processes in complex socio-ecological landscapes in the tropics. In particular, few attempts have been made to combine, in a single approach, various human-mediated effects on the spatio-temporal propagation of an invading pest population and to quantify their relative importance (but see Prasad et al. 2010 in North America). Even scarcer are the field data, especially in tropical countries, required to validate the dynamics in invasion processes. In this contribution we address the issue of modeling exotic pest invasion in the tropical Andes, a region transformed by anthropogenic systems into a mosaic of agro-ecosystems at different stages of succession and different levels of human influence (Ellenberg 1979). Propagation of invasive species may be facilitated by intensified road construction that reduces the naturally high isolation and low connectivity of mountain environments (Pauchard et al. 2009). In our case, road rehabilitation into an isolated valley constituted an exceptional natural experiment to study the propagation into a previously non-infested landscape of the potato tuber moth (*Tecia solanivora*, Povolny, Lepidoptera: Gelechiidae). Actual moth propagation data obtained through participatory monitoring (Dangles et al. 2010) suggested that the speed of the invasion in the valley was not possible through diffusion dispersal only, given that tuber moths are weak fliers (Cameron et al. 2002; Mesías and Dangles, pers. obs.). The specific aim of our study was therefore to investigate the role of human activity on the spatio-temporal invasion

dynamics of an emerging agricultural pest. For this, we employed a spatially explicit, CA model that accounted for the influence of crop storage structures that modify the thermal environment for the pest (Dangles et al. 2008) and of passive, long-distance transport of insects in human vehicles. Our study showed how pest colonization and propagation on mountainous agricultural landscapes in the tropics are influenced by these human activities, and that they should be acknowledged when designing pest management strategies. While we exclusively focus on potato moths in the tropical Andes in this paper, our approach is applicable to a much wider geographic range (most agricultural ecosystems) and to introductions of other ectothermic organisms.

Materials and methods

Study organism and site

The Guatemalan potato tuber moth, *Tecia solanivora*, is an invasive pest whose larvae attack exclusively *Solanum tuberosum* L. tubers both in the field and in potato stocks. *T. solanivora* has been successfully invading the northern Andes within the last 30 years (Puillandre et al. 2008). During the last decade it has been considered one of the major pests for potatoes in Central American and Northern South American countries (Dangles et al. 2009). Infestation is often highest (up to 90%) in traditional potato storage structures (tubers heaped under a basic shelter), which offer optimal conditions for moth development (Dangles et al. 2008).

We studied the spatio-temporal expansion of *T. solanivora* in the valley of Simiatug (Central Ecuador, Fig. 1a) which constitutes a prime example to understand species invasion dynamics. Before 2005 moth introduction and propagation into the valley was virtually impossible because of two reasons. First, it is surrounded by large areas of natural páramos (herbaceous ecosystems of high altitude, mainly above 3,800 m) and natural or cultivated forests, all unsuitable for moth survival (Fig. 1b). Second, due to the lack of roads, commercial activities with villages outside the valley were limited. In 2006 road sections from Guaranda northward to Salinas were rehabilitated enhancing commercial exchanges and allowing *T. solanivora*'s arrival and propagation (Dangles et al. 2010) (Fig. 1b).

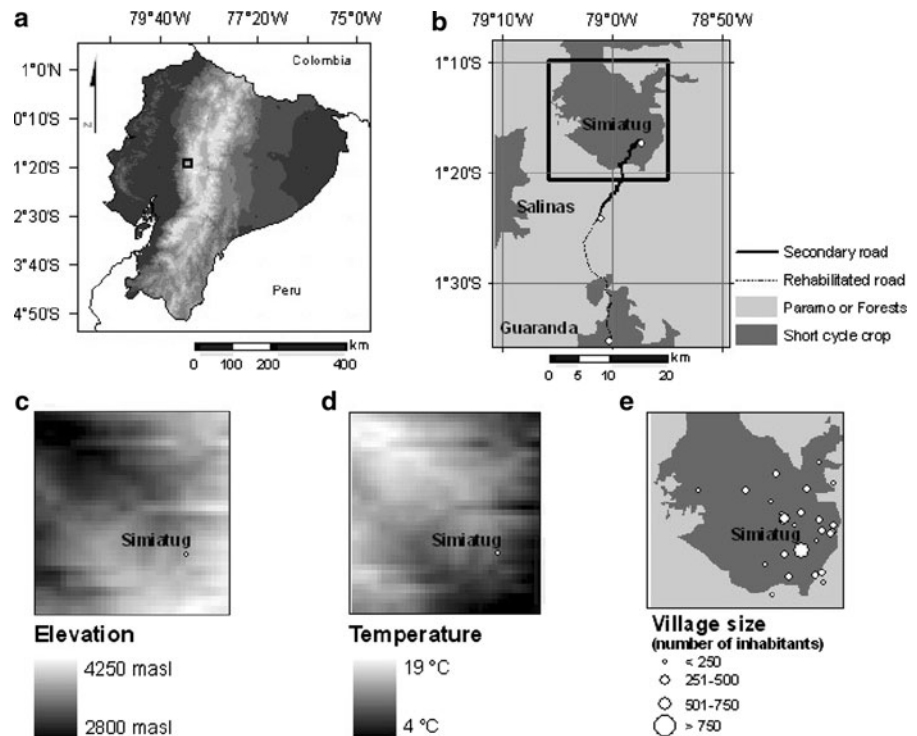
Altitudes of the Simiatug valley range from 2,800 to 4,250 m (Fig. 1c). Its climatic conditions are typical of the Ecuadorian Andes where mean temperatures vary more with altitude than with season (Fig. 1d) (Dangles et al. 2008). Diurnal temperatures vary dramatically and the pattern of hot days and cold nights overshadows temperature variations through the year. Rainfall also shows little seasonality and varies on a local basis (see climate graphs in Dangles et al. 2008, Appendix A, <http://www.esapubs.org/archive/appl/A018/062/appendix-A.htm>). Such stable climatic conditions permit potatoes to be grown all year, and cause the agricultural landscape to be made up of a mosaic of potato fields at various stages of maturation. This, along with the presence of stored potato tubers in traditional shelters, means that food for moth larvae is always available. These conditions likely explain why neither diapause nor seasonal rhythms have been reported for this species at any elevation in Ecuador and imply that its thermal limits and population dynamics are defined spatially rather than seasonally (Dangles et al. 2008). About 25,000 people, mainly subsistence and market-oriented farmers, currently live in the Simiatug parish in about 45 Kichwa communities or in scattered houses across the territory. With approximately 3,000 inhabitants, Simiatug village is the economic center of the valley and the communities around are smaller in size and density (50–700 inhabitants) (for further detail see Dangles et al. 2010).

The model

Overall structure

Potato moth dynamics were simulated with a spatially explicit, stage-structured, CA model, based on biological and ecological rules derived from field and laboratory data of *T. solanivora*'s physiological responses to climate (temperature and rainfall). Our simulations focused on a study area of 20 × 20 km within the valley (Fig. 1b) represented by a grid of 1,600 cells with a cell size of 0.25 km². Each cell of the grid is characterized by environmental variables such as temperature, precipitation, land use and the presence and size of villages (Fig. 1e) (MAE and EcoCiencia 2005; Hijmans et al. 2005). Cell size was selected to match the resolution at which land use data were available.

Fig. 1 Map of the study area showing **a** the location of the Simiatug Valley in the central Ecuadorian Andes; **b** land use in the area showing the specific area of 20×20 km of our cellular automaton (black square); **c** elevation of the cells of our grid; **d** mean yearly temperature of the last 30 years of the study area; and **e** villages in the study area. See Fig. 4 for known moth distribution in the Simiatug valley from 2006 to 2009)



Model formulation

In this section we briefly describe our model's formulation. For more detail see Appendix S1 in Supplementary material. Our model's setup consisted of an initial inoculum of 90 moths in Simiatug village, the main source of moth infestation in the region (Dangles et al. 2010). The choice of this inoculum was based on measurements by our team of moth abundance in infested potato sacks. However, sensitivity analysis showed that varying this parameter had no effect on model output (see Appendix B in Rebaudo et al. 2010). Each time step represented one *T. solanivora* generation (normalized to 3 months at 15°C). During each step we used a stage-structured model (Briggs and Godfray 1996; Miller 2007) to describe moth population dynamics in each cell. Three biological processes governed these dynamics: survival (both demographically based and climate dependent) between each consecutive stage, dispersal through diffusion (density dependent) and reproduction (climate dependent). Each time step the infestation grew and spread over farmers' fields.

An important assumption of our CA is maximum moth passive dispersal distance. We are not aware of any empirical data on *T. solanivora*'s flight capacity.

We therefore used data of a related moth, *Phthorimaea operculella* (Gelechiidae), the only published data we are aware of. However, even for *P. operculella*, there is little and contradictory information regarding its flight abilities, with some studies describing these moths as good fliers (Yathom 1968; Foley 1985) and others reporting limited flight abilities (Fenemore 1988). In two separate studies, Cameron et al. (2002, 2009) reported that these moths could fly up to 250 m. We therefore used this value for our maximum dispersal distance parameter. Comparative observations by our team of flight capabilities between *P. operculella* and *T. solanivora* in Ecuador revealed that the latter is a much worse flier than the former and we thus considered that we did not underestimate *T. solanivora*'s dispersal ability. Furthermore, a closer look at *T. solanivora*'s propagation into the Simiatug valley revealed that in order to predict the observed pattern of invasion without long distance dispersal, moths would have to fly about 1.5 km per generation, a value six times higher than the one chosen for our parameter.

To avoid populations growing to unmanageable sizes we set adult moth carrying capacity of each cell to 1,000 individuals. This value corresponds to the

highest number of moths ever collected in the Ecuadorian Andes by the staff of the Laboratory of Entomology of the PUCE in an area of 250 m of radius, the action range of pheromone traps (Barragán comm. pers.). Furthermore, it lies within the range of observed densities of adults of other Gelechiidae (see Rothschild 1986 and references therein). To ensure that this did not impact our results we ran a sensitivity analysis where carrying capacity was varied and found that this parameter had no effect on dispersal speed but had a strong effect on population growth (results not shown, but see Appendix B in Rebaudo et al. 2010). However, since our output was expressed as “relative moth abundance” (see “[Analysis of moth propagation](#)” section), results were not affected by the carrying capacity.

We built on this basic scenario to incorporate the effects of two key farmer activities on moth propagation identified in previous studies: (1) changes in microclimatic conditions due to presence of potato storage structures (Dangles et al. 2008), and (2) long-distance dispersal (LDD) events through passive moth transportation in human vehicles (Dangles et al. 2010).

Potato storage structure scenario

Potato storage structures have been shown to buffer extreme air temperatures (see Dangles et al. 2008, Appendix D), changing the thermal environment of the growing larvae. To further understand the importance of these structures for moth invasion dynamics, we surveyed temperature conditions inside and outside potato storage structures using data-loggers (HOBO® U12, Onset Computer Corporation, Pocasset, MA, USA). For details see Appendix S2 in Supplementary material.

To examine the influence of storage structures on moth dynamics we located structures in 0, 15, 30, 45, 60, 75 or 90% of the cells of the CA, with three different types of spatial distribution (aggregated, random, and regular). Several procedures are available to generate particular point patterns in a two dimensional space (Wu et al. 1987; Diggle 2003; Perry 2004). We used the R “spatstat” package which allows the creation of point patterns with distributions from aggregated, through random to regular (Baddeley and Turner 2005). We generated the aggregated distribution, using a Neyman–Scott process with the “rneymanscott” function, the random distribution

with a homogenous Poisson process, using the function “rpoispp”, and the regular distribution with a Simple Sequential Inhibition (SSI) process with the “rSSI” function.

To characterize the general form of the inside-outside temperature relationship (Fig. 1 of Appendix S2) we fitted the data to a linear and three non linear functions (log, power and hyperbole). The linear relationship gave the best overall fitting performance and was thus used to modify the temperature of cells with storage structures as follows:

$$T_{Si} = aT_{Oi} + b \quad (1)$$

where T_{Si} is temperature inside the storage structure at cell i and T_{Oi} is mean outside air temperature of that cell. The values of parameters a and b depend on cell altitude (see Table 1 of Appendix S2).

Long-distance dispersal scenario

Long-distance dispersal through human transportation of potato tubers, re-used potato bags and infested soil (using motorized vehicles, donkeys, or llamas as transportation agents) constitutes a key mechanism for potato moth spread in the Andes (EPPO 2005; Dangles et al. 2010). LDD was included in our CA by using a gravity model. These models are a common tool, mainly used by geographers, which allow the estimation of LDD between discrete points in heterogeneous landscapes (Bossenbroek et al. 2001). They relate the interaction strength between a discrete invading source and an invaded destination and calculate the flow of individuals that move from one to the other (Muirhead et al. 2006). Following the approach developed by Bossenbroek et al. (2001) we modeled the probability of moths jumping from an infested village i to an uninfested one j ($P_{i \rightarrow j}$) as follows:

$$P_{i \rightarrow j} = \sum_{i=1}^{26} [W_i * \eta_i] * \left[\frac{W_j}{z_j} \right] \quad (2)$$

where the first factor represents the probability of a vehicle carrying infested potatoes leaving an infested village, and the second one represents the attractiveness of a non-infested village (note that there were 26 villages in our study area). The first factor is influenced by village size (human population relative to that of Simiatug village, $W_i = \text{Pop}/3,000$) and the relative abundance of moths (η_i) in that cell (relative to

cell carrying capacity, i.e. 1,000). The second factor is influenced by village size (Gilbert et al. 2004) and relative remoteness (z_j). Remoteness was calculated as the total time to travel from one village to all the others (Dangles et al. 2010). Each village had its own relative remoteness value (z_j) which was obtained by dividing village remoteness by the value of the most remote village. We chose not to include distance between villages in the equation since the probability of farmers visiting a village depends on the time it takes for them to get there (which is influenced by the existence and quality of roads) rather than on actual distance. Establishment (sensu Liebhold and Tobin 2008) in a newly invaded cell depends on the environmental characteristics of the sink cell. Thus, moths have some probability of arriving to any cell with a village but the probability of them establishing there depends on the climate and the presence or absence of potato cultures in it. As the invasion evolves more villages become infested and the number of moths in each increases. As a consequence, the probability of moths dispersing to uninfested villages also increases.

As the success of an invading population is known to be highly affected by the number of propagules which is involved in the LDD event (see the notion of “propagule size” effect in Liebhold and Tobin 2008), the importance of LDD for invasion dynamics was assessed by varying the number of moths potentially jumping from one village to another during each time step of the CA. Simulations were performed for propagule sizes of 0, 10, 20, 40, 80, 160, 320, or 640 juvenile moths.

In this contribution we assumed that propagule size was fixed in each simulation (i.e. the number of moths that jumped was the same during each LDD jump). This is not the case in reality where the number of organisms that disperse varies between each dispersal event (Liebhold and Tobin 2008). An interesting future research perspective would therefore be to analyze the effect that varying the size of the propagule during each inter-village transfer has on model output.

Analysis of moth propagation

The model allows simulating moth propagation in the study area through time. (Figure 2a–c shows captions of CA grids with the temporal evolution of T .

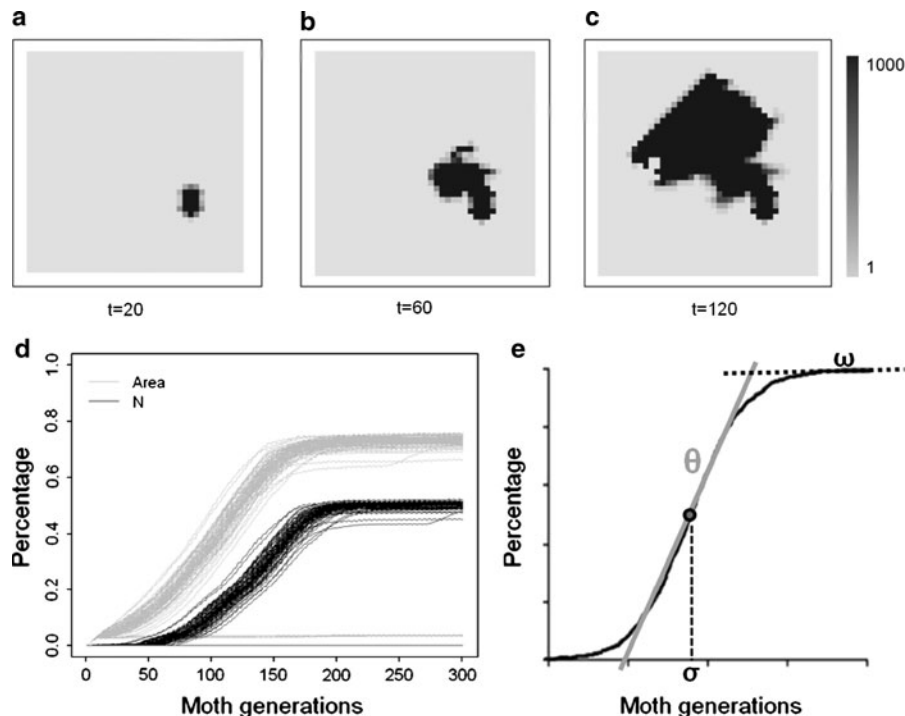
solanivora levels at three different steps of the invasion process.) As model output, we were interested in the progression of moth relative abundance and of the proportion of invaded area through time (black and gray curves of Fig. 2d, respectively). Since both types of output presented similar results we will refer only to moth abundance data in the following. Model output was adjusted to the following sigmoid function (Hufkens et al. 2008) as follows:

$$n(t) = \frac{\omega}{1 + e^{-\theta(t-\sigma)}} \quad (3)$$

where ω represents the proportion of moths (relative to the total carrying capacity of the model, i.e. 1,600,000 moths) where the invasion stabilizes, θ the steepness of the curve (i.e. invasion speed) and σ the generation at the invasion’s mid-point (Fig. 2e). Parameters were estimated with the “nls” function in the “stats” package of R (R Development Core Team 2009 version 2.10).

We used boosted regression trees, BRT (Elith et al. 2008; Buston and Elith 2011; Munkemüller et al. 2011), to understand the relative contribution of each factor on model output. For this we ran simulations with all the possible combinations of parameters’ values among the human influence factors (i.e. we combined the different percentages of storage structures, with the three types of storage structure spatial distribution and with different propagule sizes). We ran 20 simulations for each combination. Then we adjusted Eq. 3 to model output and ran the boosted regression tree analysis on each of the three parameters. BRTs were fitted in R (R Development Core Team 2010 version 2.11.1), using gbm package version 1.6-3.1 (Ridgeway 2010) plus custom code that is available online (Elith et al. 2008). We calibrated our boosted regression tree models through a 10-fold cross validation (CV) and determined optimal number of trees by systematically varying values for tree complexity, tc , and learning rate, lr , and choosing the number of trees where holdout deviance was minimized. We used partial dependence plots to visualize the influence of parameters on the model’s output. These plots show the effect of a focal predictor on the response controlling for the average effect of all other variables in the model (for further information on boosted regression trees and an explanation of their parameters see Elith et al. 2008, and Buston and Elith 2011).

Fig. 2 Examples of model outputs: **a–c** spatial invasion represented by captions of CA grids at three different steps (t) of the invasion process; **d** temporal invasion throughout moth generations with the relative number of moths (N) and the proportion of invaded area (Area); **e** sigmoid wave showing the parameters used in the sensitivity analysis



Model validation with field data

Spatio-temporal validation of the invasion process in the Simiatug valley

A four year survey of PTM abundance since the initial introduction of the pest into the Simiatug valley in 2006 allowed us to compare the spatio-temporal invasion simulated by our model to real data. These data were obtained once a year from participative monitoring with local farmers from 13 communities located at various altitudes and distances from Simiatug village (see Dangles et al. 2010). We compared the agreement between observed data and either the basic or the LDD scenarios' outputs after 16 generations (i.e. 4 years), with the use of the kappa statistic which measures the proportion of correctly predicted presences and absences, after accounting for chance effects (Manel et al. 2001). We further examined the significance of kappa values under the null hypothesis of no agreement beyond chance (Fleiss 1971). These analyses were performed using the “PresenceAbsence” package of R (R Development Core Team 2009).

Altitudinal validation in the Ecuadorian Andes

We compared moth altitudinal distribution predicted by our model (using the altitudes of the cells infested by *T. solanivora* at equilibrium) with data of the actual distribution of the pest in the country. This analysis allowed us to assess the validity of our model in predicting the actual spatial distribution in agricultural landscapes of the Ecuadorian Sierra. Data from 80 sites were obtained through a large-scale field survey in four provinces in the center of Ecuador (Cotopaxi, Tungurahua, Chimborazo, and Bolívar) at altitudes ranging from 2,300 to 3,700 m (see <http://www.innomip.com> for further details on moth monitoring in the region). At each site, the abundance of *T. solanivora* adult males was monitored using dome traps baited with pheromones and placed at 1 m height in potato fields. Catches in traps were recorded every 3 weeks during at least the 10 weeks that preceded harvest date (see Dangles et al. 2008, for further details). We compared the observed data to the distributions of the frequencies of the altitudes of cells with moth predicted by (1) the basic, (2) the LDD, and (3) the LDD and storage structure scenarios combined

(LDD + storage) through Kolmogorov–Smirnov (K–S) tests. We also compared the means and variances of the distributions with a Welch Two Sample *t* test and an *F* test, respectively. All these analyses were performed with R (R Development Core Team 2009).

Results

Model exploration: influence of human practices on moth dynamics

Influence of potato storage structures

As evidenced by the boosted regression tree analysis, storage structure distribution had a stronger influence on the relative number of moths at the end of the invasion process (i.e. parameter ω , Fig. 3a) with clumped distribution allowing higher moth densities than the two other types of distributions. Storage structure percentage influenced moth abundance less strongly (Fig. 3b), but analysis did show that these two variables presented a positive relationship, with moth abundance increasing with higher percentages of storage structures.

Contributions of each human influence factor on parameter θ were similar (Fig. 3d–f) with storage structure distribution presenting a slightly stronger influence than the other two. Invasion speed increased from clumped to random and to regular distribution (Fig. 3d). On the other hand, this parameter decreased as storage structure percentage increased (Fig. 3e). However, these results are probably artifacts due to the fact that with clumped distribution and with higher storage structure percentages moth final abundance is higher, and reaching this higher number of moths takes more time.

The generation at invasion midpoint (i.e. parameter σ) was also influenced in a similar degree by the three parameters (Fig. 3g–i). Differences among the three types of storage structure distribution were less evident, with a slight decrease from clumped to regular (Fig. 3g). Increasing storage structure percentage caused generation at invasion midpoint to increase (Fig. 3h), but again this is due to the increase in final moth abundance.

Influence of long-distance dispersal

The influence of propagule size on moth abundance was low and did not vary among the different numbers

of moths that jumped (Fig. 3c). This was expected since propagule size does not influence the amount of invadable space and when the invasion stabilizes cells have reached their carrying capacity.

Our analysis showed that including LDD jumps accelerated the invasion process, as evidenced by the increase in parameter θ (Fig. 3f) and the decrease in σ (Fig. 3i). LDD influenced parameter σ to a slightly higher extent than the two factors related to storage structures (Fig. 3i). However, we found that our model was insensitive to varying propagule size. All the difference was concentrated between simulations with no LDD and simulations with LDD. This is probably caused by high moth fecundity (a female moth lays more than two hundred eggs at 15°C), as when moths jump invaded cells soon reach their carrying capacity, diluting initial differences in propagule size.

Model validation

Spatio-temporal validation in the Simiatug valley

The level of agreement of the basic model and LDD scenario with field survey data at 13 villages across the valley is shown in Fig. 4. We found that the inclusion of LDD in our model provided a better prediction of *T. solanivora*'s spatio-temporal propagation through the Simiatug valley, as revealed by the higher values of kappa. However, these values were significant only for 2007 and 2008. In 2009 the value of kappa is lower because the model predicts moth presence in village 9 although they were not found during the monitoring. The basic model did not predict moth presence in six of the villages where the insects were found during field monitoring. In some of them, notably villages 5 and 6, the model predicted moth presence only 4 years after the invasion, suggesting an unrealistically slow dispersal (Fig. 4b). In contrast, the LDD scenario was able to predict moth presence in almost all villages where moths were found during the monitoring (Fig. 4c). In village 2 the LDD scenario did not predict moth presence, and moths were not observed during monitoring along the 4 years. This village is unsuitable for moth survival because of the absence of potato cultures (no suitable habitat). Village 11 was the only one where our LDD model did not predict moth presence even though moths were found during the monitoring. Other small discrepancies between our LDD model prediction and field data mainly consisted

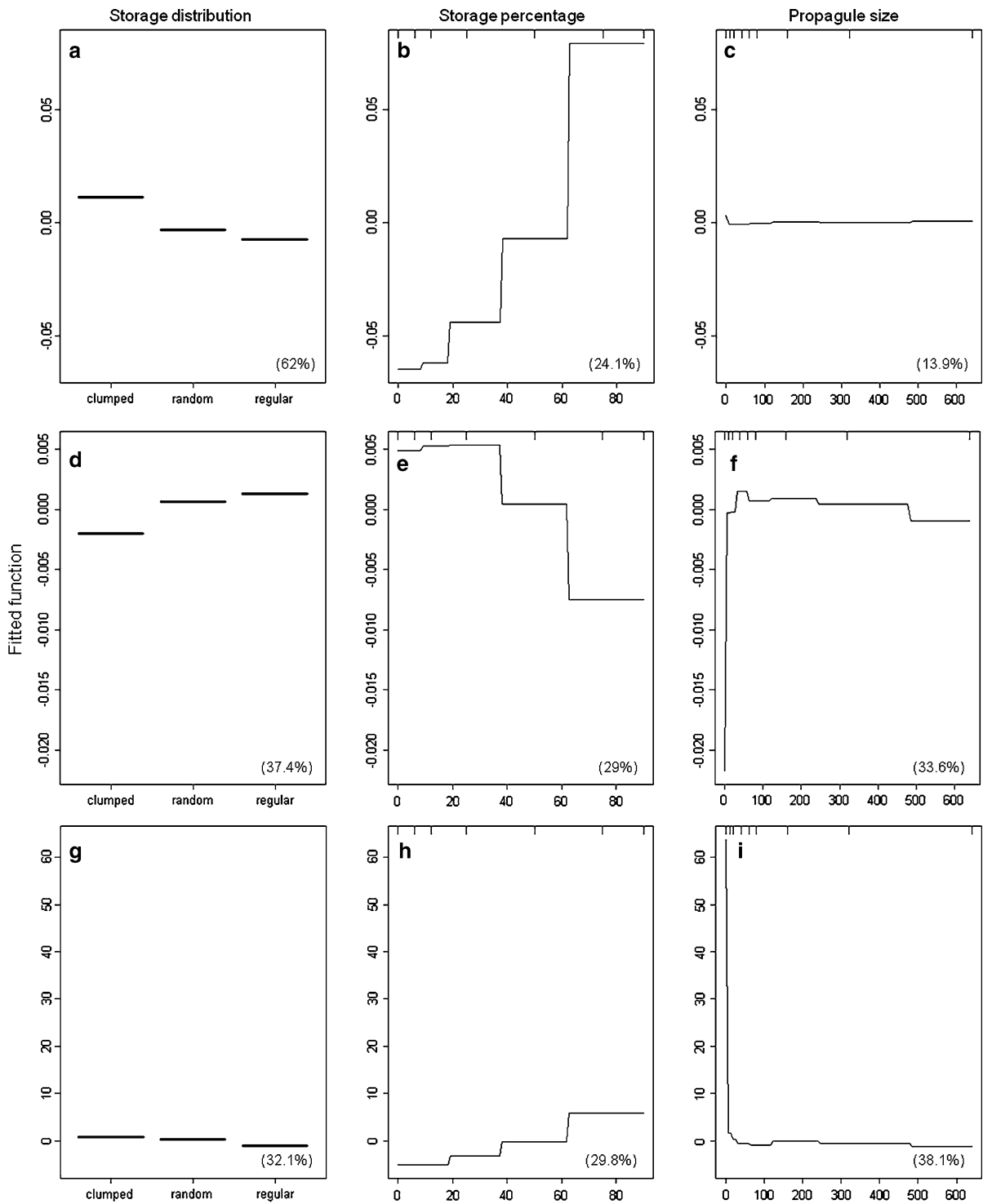
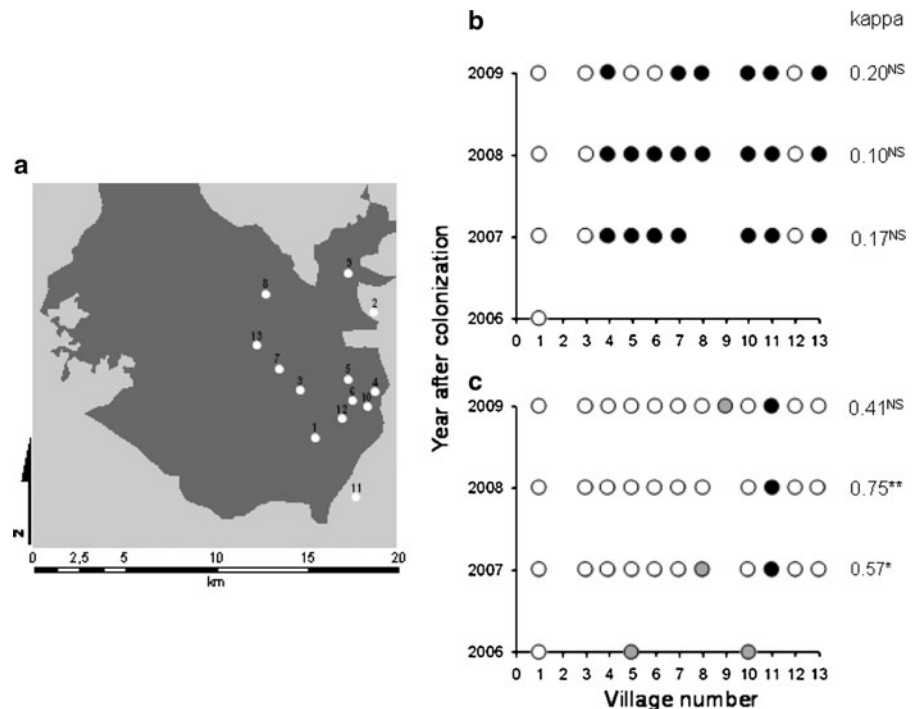


Fig. 3 Partial dependence plots for parameter ω (a–c), θ (d–f), and σ (g–i). Fitted functions have been centered by subtracting their mean. Rug plots at the inside top of plots show the

distribution of data, in deciles, of the variable on the X-axis. Values in parenthesis indicate relative contribution of each factor to model output

Fig. 4 Spatio-temporal validation of the model's outputs to field monitoring data from 2006 to 2009 in the Simiatug valley. **a** The 13 villages involved in the monitoring; **b** outputs of the basic model (no human influence); **c** outputs of the LDD scenario. *Black circles* represent cases where moths were observed but not predicted by the model; *gray circles*, cases where moth presence was predicted by the model, but no moths were found during the field monitoring; and *white circles*, cases in which model outputs coincided with field data



in a prediction of moth arrival in the villages before they actually did arrive.

Altitudinal validation in the Ecuadorian Andes

We compared moth altitudinal distributions predicted by our model at stable population levels with those found under field conditions (Fig. 5). Distributions of the basic and LDD scenarios were virtually identical (K–S test: $D = 0.08$, $P = 1$), because LDD accelerates the invasion but does not allow moths to survive in cells with unsuitable climate. We also found that these results were no different from the distribution of observed data (K–S test: $D = 0.38$, $P = 0.291$), implying no significant differences between our predictions and field data. Distributions predicted by the LDD and storage structure scenarios combined was also not different from the observations (K–S test: $D = 0.15$, $P = 0.998$). However, t and F tests showed that with respect to mean and variance the LDD plus storage structure scenario was more similar to the observed data than the LDD and the basic scenarios (t test P value = 0.992, 0.631, and 0.553 and F test P value = 0.942, 0.695, and 0.688, respectively).

Discussion

Spatial heterogeneity plays a defining role in population dynamics (Hutchings et al. 2000; Hanski and Gaggiotti 2004), and several authors recognize the importance of its inclusion into studies of biological invasions (Melbourne et al. 2007; Jongejans et al. 2008; Harris et al. 2009; Carrasco et al. 2010). Heterogeneity may be caused by variations in abiotic factors such as temperature or precipitation, or in biotic factors such as resource availability or the presence of competitors (Schreiber and Lloyd-Smith 2009). Our work suggests that another type of spatial heterogeneity, socially induced heterogeneity, is probably one of the main drivers of invasion dynamics in agricultural landscapes.

Spatially explicit, stochastic modeling methods are useful for simulating the influence of spatial heterogeneity on invasive dynamics (Nehrbass and Winkler 2007; Nehrbass et al. 2007; Travis et al. 2011). CA models, in particular, allow including detailed information about the landscape—making it not simply spatially explicit, but spatially realistic (Harris et al. 2009)—and are especially useful for simulating dynamics in landscapes with particular structures

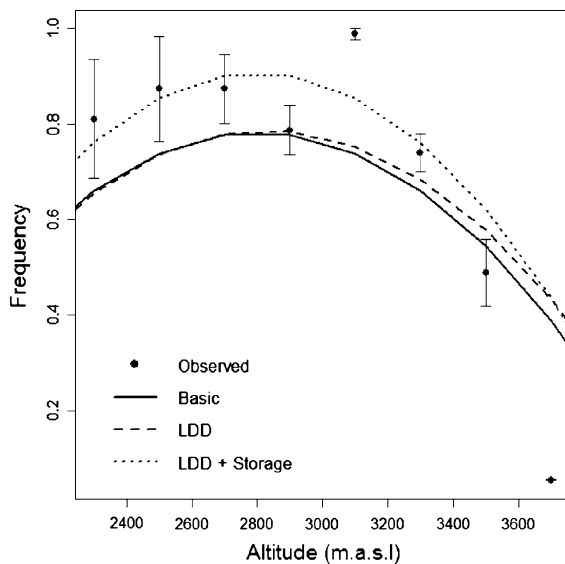


Fig. 5 Altitudinal validation of the model's outputs to field monitoring data in the Ecuadorian Andes. The figure shows the comparison between the observed altitudinal distribution in 85 sites of central Ecuador where moth abundance was sampled between 2006 and 2009 and predicted distribution by the model's basic (no human influence), LDD and LDD plus storage structure scenarios. Bars indicate 95% confidence intervals on observed frequencies

(Soons et al. 2005; Herben et al. 2006; Jongejans et al. 2008). In this study, incorporating real-world data bases of environmental and social variables into the model proved a powerful tool to simulate invasive spread in a human-dominated landscape.

Modification of the climatic environment by storage structures

Given the influence of temperature on insect population dynamics, their propagation may be enhanced if they encounter sites with suitable thermal conditions (Régnière and Turgeon 1989). Several studies have acknowledged the buffering capacity of storage structures and their influence on potato tuber worm survival (Roux and Baumgartner 1998; Hanafi 1999; Keasar et al. 2005), but recognize that data concerning the ambient temperature in storage structures is lacking (Keasar et al. 2005). Our temperature surveys helped us to better understand the actual temperature buffering capacity of storage structures in our landscape. They revealed that below altitudes of 3,100 m potato storage structures present microclimatic

conditions always favorable for infestation by *T. solanivora* while above 3,100 m these structures usually present unfavorable microclimatic conditions (temperature inferior to field temperature and between 9 and 10°C). Our results showed that, in general, storage structure presence increased moth abundance and that spatial distribution of storage structures has a strong influence on moth dynamics with a clumped distribution being the most favorable to moth survival and propagation. Moth's altitudinal distribution predicted by our model when we included storage structures was closer to the species' actual distribution than that predicted by the basic or LDD scenarios. Hence, it seems that potato storage structures permit moths to survive in sites from which they would normally be excluded due to climatic constraints. This result is consistent with those of Suarez et al. (2001) and Pitt et al. (2009) who found that the invasion of the Argentine ant, *Linepithema humile*, was always positively affected by the presence of human constructions (notably human habitations) that allow them to persist locally in areas with unfavorable climates. However, we also found that a high density of storage structures was detrimental for moth invasion above 3,100 m (results not shown), certainly due to the persistence of cold temperatures (ca. between 9 and 10°C) within the storage structures located at such altitudes. Since Simiatug village (where we placed the initial inoculum) is located at 3,400 m, high storage structure density at and around this location may drastically slow or impede moth survival, causing a severe decrease on the relative number of moths in some of the simulations. This counterintuitive result coincides with results found in a study at the Mantaro Valley (central Peru) where farmer interviews revealed that some high altitude storage structures were not infested by the potato tuber moth, *Symmetrischema tangolias*, probably due to the low temperatures attained by these structures (Keller 2003).

Long-distance dispersal events

Our results highlight the importance of passive moth transportation in human vehicles which allows insects to make LDD jumps. Even though several authors have acknowledged the significance of this type of dispersal for species' spread (Buchan and Padilla 1999; Bossenbroek et al. 2001; Nehrbass et al. 2007), notably invasive insects (Suarez et al. 2001; Pitt et al.

2009; Carrasco et al. 2010), its inclusion in models still poses difficulties for modelers (Bossenbroek et al. 2001; Pitt et al. 2009). The failure to accurately measure LDD events has impeded sufficient agreement between model output and empirical data (Hastings et al. 2005). Most dispersal models are based on empirically measured rates of dispersal which are not available for many species. Even when such data are available, these types of models may underestimate spread rates since they do not allow organisms to jump over unsuitable habitat (Pitt et al. 2009). Classical metapopulation models (Hanski et al. 2000), SPOMs (Moilanen 2004) or gravity models are suitable in such cases. The latter represent an interesting choice for modeling LDD in the case of species for which no data on the rate of long-distance jumps are available. These models do not consider movement rates by organisms themselves, but the force of attraction between an origin and a destination (Bossenbroek et al. 2001). Thus, they may be quite useful to predict the spread of human-vectored organisms where site ‘attractiveness’ is based on human behavior (Gilbert et al. 2004; Carrasco et al. 2010).

Modeling *T. solanivora*’s long-distance jumps with a gravity model was suitable since passive transport in human vehicles is thought to be the means by which these organisms attain far away sites (EPPO 2005). A key step when using these types of models consists in including the appropriate set of factors likely responsible for the dispersal of the invasive species (Bossenbroek et al. 2001). In our case, including village size and remoteness as measures of interaction force permitted us to accurately simulate moth spread across the valley. This reveals how social heterogeneity plays an essential role defining the patterns of propagation of invasive pests in human dominated landscapes. Including the gravity model within the CA was certainly convenient since the latter allowed us to “spatialize” such heterogeneity and enhanced realism in our predictions.

In some cases, our LDD scenario over estimated invasion speed by predicting moth dispersal to some villages where they have not been detected with the field monitoring or before they actually were. This may be related to the stochastic nature of jump dispersal events (Lewis and Pacala 2000) that we incorporated in our model by making the probability of LDD equal to a product of two other probabilities (the probability of moths leaving a village by the

probability of moths arriving to another, Eq. 1). However, as pointed out by Pitt et al. (2009) overestimation in such models means that they may be used for risk assessments of invasion since they allow the localization of invulnerable sites.

Potential application for invasive pest control in tropical agricultural landscapes

Accurate predictions of pest invasion dynamics are important for people concerned with integrated pest management (IPM) to optimize the type, place and timing of control measures used to minimize the damages (Régnière et al. 2009; Shea et al. 2010; Travis et al. 2011). Our CA model allowed us to understand the influence of human practices on pest propagation, and provided direct applications for pest management such as the importance of surveying farmers’ storage structures’ temperature regimes to assess their potential role in insect persistence and spread. A further advantage of CA models is that they can be easily coupled with agent-based models (Bonabeau 2002), which allows taking farmer behavior directly into account to simulate its impact on insect spread. Recently, we integrated our CA with an agent-based model to assess the importance of farmers’ mobility and pest control knowledge on pest expansion (Rebaudo et al. 2011). Such a coupled model was then used as an educational tool to make farmers aware of the dangers due to the pest and on the procedures they should follow to impede its propagation. The flexible and upgradeable nature of CA would make them powerful tools for ecologists to better understand invasion dynamics in the most challenging landscapes.

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