THESIS

to obtain the degree of

DOCTOR OF PHILOSOPHY

OF THE UNIVERSITY PARIS VI – PIERRE ET MARIE CURIE

Specialization: DIVERSITY OF THE LIVING WORLD

presented by

María Verónica CRESPO-PÉREZ

Global changes and distribution modeling of invasive insect pests in the Tropical Andes

Defended on January 11th 2012

in front of the jury composed by

M. Olivier DANGLES, DR, IRD	Supervisor
Mme. Isabelle CHUINE, DR, CEFE	Co-supervisor
Mme. Christelle SUPPO, DR. IRBI	Rapporteur
M. Hervé JACTEL, DR, INRA	Rapporteur
Mme. Martine MAIBECHE-COISNE, DR, UPMC	Examinateur
M. Roger ARDITI, DR, INA-PG	Examinateur
M. Justin TRAVIS, DR. Univ. Aberdeen	Examinateur

para mi abue Vevita,
con todo mi amor

ACKNOWLEDGEMENTS

First and foremost I would like to express my most sincere gratitude to Olivier Dangles. From the beginning of my career you believed in me and encouraged me to pursuit my studies in ecology. Your love for science and your enthusiasm have motivated me to continue in this path. Thank you for being a guide and true mentor.

Also I would like to thank the DEEIT team of the IRD, especially Jean-Francois Silvain, for their hospitality during my stay in Gif and their interest in my work.

I would also like to express my thankfulness to Isabelle Chuine for welcoming me into her team at the CEFE, Montpellier. Working with you and your team was a truly enriching learning experience.

I am extremely grateful to Jacques Régnière for sharing his knowledge with me on insect phenology modeling and for making my stay in Quebec very productive and fruitful. For his useful advice always accompanied by a great sense of humor and enthusiasm.

I am thankful to François Rebaudo for introducing me to cellular automata, for his help during model development and analysis, for sharing his knowledge of R with me and for his hospitality during my time at Gif.

Equal thanks go to Rémi Saint Amant for his help developing the phenology model, for always being available when I had questions or problems and for his time and hospitality and for being the best tourist guide I could have asked for in Quebec.

My friends at the CEFE Montpellier, Manu, Sylvain, Fred, Tanya, and above all Benedicte, David and Ambalika for opening their home for me and for filling my last months in Montpellier with love, laughter and good times.

My friends in Montpellier, especially Elodie Blanchet for her sincere friendship, hospitality, support and good humor and for including me in her busy weekends travelling through France.

I am grateful to Catherine and Jean Pohu for receiving me in their home during my time in Gif, filled with good times, delicious food and a little bit of Spanish.

The Ormaza family in Paris for always having their doors opened for me, for their support, for making me feel like one of their own and for their constant interest in my work and life during my stay in France, and even afterwards!

My friends in Quito and abroad, los entomolocos y los no tanto, for their encouragement, advice, patience and for always believing in me, helping me and rooting for me during rough times. Especial thanks go to Paula Iturralde for her always enthusiastic help with some technical aspects of the PhD and her unconditional friendship, support and loyalty.

I am most grateful to my parents for their love, their trust, their patience and for giving me the strength to continue even when I was feeling weakest. My sister and brother for their love and friendship and for always being there with their good humor and advice. My niece, my nephew, my grandmothers, aunts, uncles and cousins for their love and constant support.

Last but not least, I want to thank the French Embassy in Quito and the DSF (Département Soutien et Formation des Communautés Scientifiques du Sud) of the IRD for their funding, without which this PhD project would have not been possible.

ABSTRACT

Physiology, behavior, abundance and distribution of ectotherms, such as insects, are highly influenced by temperature. Knowledge about their responses to temperature allows the development of simulation models that mimic their spatio-temporal dynamics. These constitute important tools for invasive pest management as they allow identification of vulnerable zones and an accurate timing and placement of control measures.

In this study we tackled the issue of modeling the spread and distribution of three species of invasive Potato Tuber Moth in the highly heterogeneous North Andean Region. We developed modeling approaches that allowed us to overcome common difficulties associated with modeling invasive dynamics in this region. First, we developed a spatially-explicit cellular automaton that simulated moth spatio-temporal propagation while taking into account the influence of human activity on moth spread. We also developed models capable of accounting for the influence of thermal variation on moth dynamics and of simulating dynamics even when adjusted to small data sets. Finally we developed an individual based model that simulated PTM temperature-related dynamics and was used to construct current and future pest risk maps at the scale of the North Andean Region.

This work revealed the importance of both human-induced and environmental heterogeneity as drivers of PTM invasion. Including biotic interactions, as well as more detail in environmental and social heterogeneity constitute interesting perspectives that could enhance the realism and accuracy of future modeling approaches in the region. The methods developed in this thesis could constitute important tools for integrated pest management since they may help to enhance farmers and stakeholders' understanding of the threats posed by these pests and raise their awareness about the influence of their actions on pests' invasion dynamics.

Key words

Agricultural landscapes, cellular automata, climate change, individual based model, invasive pests, North Andean Region, Potato Tuber Moth

RESUMÉ

CHANGEMENTS GLOBAUX ET MODELISATION DE LA DISTRIBUTION D'INSECTES RAVAGEURS INVASIFS DANS LES ANDES TROPICALES

Modélisation de la dynamique des insectes en relation avec la température

La physiologie, le comportement, l'abondance et la distribution des êtres vivants sont grandement influencés par leur environnement (Messenger 1959, Angilletta et al. 2010). Dans le cas des organismes ectothermes tels que les insectes, la température constitue un facteur environnemental clé contrôlant leur dynamique. Des études ont montré que ce facteur influence de nombreux aspects de la biologie des insectes depuis les variations temporelles de leur croissance, leur survie et leur reproduction (Angilletta et al. 2002, Savage et al. 2004, Stillwell and Fox 2005, Steigenga and Fischer 2009, Gutiérrez et al. 2010, Opit et al. 2010) jusqu'aux patrons géographiques de la taille de leur corps, de la densité de leurs populations et de la diversité et distribution des différentes espèces (Angilletta et al. 2004, Brown et al. 2004, Hodkinson 2005, Karl et al. 2008, Régnière et al. 2009). La compréhension de l'influence de la température sur la fitness des espèces permet de mieux comprendre la distribution géographique, les fenêtres temporelles d'activités et les interactions compétitives (notion de niches thermiques) des insectes en relation avec la température (Huey and Stevenson 1979). La modélisation écologique de la réponse des insectes à la température est donc une approche courante afin d'analyser et synthétiser au mieux cette information.

La réponse des insectes à la température est généralement décrite par des modèles de performance thermique. La performance est définie comme « toute mesure de la capacité d'un organisme à « fonctionner » et est généralement exprimée comme un taux ou une probabilité » (Angilletta 2009). Des mesures usuelles de la performance thermique sont la survie, le développement, la croissance, la fécondité, la locomotion, l'assimilation et le fourragement (Gilchrist 1995, Angilletta 2009). Les modèles de performance thermique consistent en des fonctions mathématiques qui décrivent la relation entre la température et une mesure de la performance des insectes, chaque mesure ayant généralement une fonction mathématique appropriée. Toutefois, dans certains cas, la même mesure de performance peut être décrite à l'aide de plusieurs fonctions différentes. La combinaison de plusieurs modèles décrivant chacun la réponse d'une mesure de performance à la température (p.ex. survie, fécondité, développement) permet la simulation de réponses complexes des organismes à la température (Angilletta 2009). Par exemple, il est possible de simuler la dynamique des populations, la phénologie ou encore la distribution d'un groupe d'individus dans le temps en construisant un modèle intégratif qui inclut les fonction de survie, développement et reproduction de ce groupe en fonction de la température (Buffoni and Pasquali 2010). L'amélioration constante des capacités computationnelles permet la construction de modèles toujours plus complexes à des échelles spatiales et temporelles toujours plus grandes (Logan et al. 2007, Régnière et al. submitted).

La plupart des êtres vivants sont confrontés à un environnement hétérogène et fragmenté, ce qui influence grandement la dynamique de leurs populations (Cadotte et al. 2006, Jongejans et al. 2008). Simuler la dispersion des populations dans ce type de paysages ou régions nécessite donc d'inclure une composante spatialement explicite dans les modèles (Sebert-Cuvillier et al. 2008, Vinatier et al. 2011). C'est le cas de nombreux types de modèles tels que les automates cellulaires (CA) (Soons et al. 2005, Herben et al. 2006, Prasad et al. 2010) qui peuvent simuler une dynamique spatiale en intégrant des cartes géographiques, ce qui les rends non seulement spatialement explicites mais également spatialement réalistes (Harris et al. 2009). Ils sont d'un intérêt majeur lorsque l'on cherche à comprendre la dynamique d'une espèce dans un paysage ayant une configuration donnée (Jongejans et al. 2008). Les modèles individus centrés (Goslee et al. 2006, Nehrbass et al. 2007, Harris et al. 2009, Carrasco et al. 2010, Travis et al. 2010, Vinatier et al. 2009, Travis et al. 2011) sont un autre groupe de modèles spatialement explicites qui présentent l'avantage d'incorporer un haut niveau de complexité démographique puisqu'ils prennent en compte chaque individu dans la population (Nehrbass et al. 2007, Jongejans et al. 2008). Ces deux types de modèles sont ainsi complémentaires pour simuler et comprendre la dynamique de propagation de population dans des régions présentant une forte hétérogénéité.

Développement de modèles dans les montagnes tropicales

Modéliser la dynamique et la distribution d'espèces dans les régions montagneuses tropicales telles que la région nord andine est une tâche difficile qui nécessite de la part du modélisateur de relever plusieurs défis. L'un de ces défis est l'importante fragmentation des paysages, principalement due à l'activité agricole (Young and Lipton 2006) qui les a transformé en de complexes mosaïques de champs cultivés. La menace majeure exercée par les espèces invasives dans ces régions souligne le besoin urgent de comprendre et prédire la distribution et la propagation de ces espèces tout en tenant compte de l'influence anthropique sur cette dynamique. Par ailleurs, la variabilité climatique dans les montagnes tropicales influence fortement la dynamique de ces espèces et doit être nécessairement prise en compte dans un exercice de modélisation. Les variations saisonnières sont pratiquement absentes des régions tropicales (Denlinger 1986, Stiling 2002, Vazquez and Stevens 2004, Dangles et al. 2008, Angilletta 2009, Grimbacher and Stork 2009) mais la diminution graduelle de la température de l'air avec l'augmentation de l'altitude (Stiling 2002, Angilletta 2009) génère une forte hétérogénéité spatiale. Cette caractéristique impose des contraintes spatiales plutôt que temporelles sur la dynamique des populations des espèces des montagnes tropicales (Dangles et al. 2008). Une autre caractéristique importante des montagnes tropicales est que la variation des températures durant la journée est généralement plus grande que la variation de la température moyenne mensuelle au cours de l'année (Denlinger 1986). L'environnement thermique subi par les insectes dans ces régions est donc fortement fluctuant et une meilleure connaissance de la façon dont les populations d'insectes sont influencées par ces régimes thermiques est d'une importance capitale afin de générer des prédictions robustes et réalistes de leur dynamique. De plus, une autre caractéristique importante des régions tropicales est le fait qu'elles englobent en majorité des pays en voie de développement (see Dangles et al. 2009a) où l'information concernant la réponse des insectes à leur environnement est généralement très fragmentaire. Ceci constitue une limite majeure pour la validation des modèles et demande une implication des modélisateurs dans la collecte de données empiriques et/ou expérimentales.

Les cartes de risques de ravageurs, largement utilisées dans le cadre de programmes de protection intégrée des cultures, décrivent la probabilité d'invasion et d'établissement de ravageurs de cultures dans une nouvelle région ou paysage. (Venette et al. 2010). Le développement de ces cartes à l'échelle régionale dans les zones tropicales de haute altitude est confronté aux défis suscités (c.à.d. à l'hétérogénéité sociale et environnement et au manque de données). De plus les prédictions d'invasions futures liées aux modifications des conditions climatiques (réchauffement global) sont confrontées à l'incertitude liée aux modèles climatiques, souvent peu régionalisés dans les zones tropicales, notamment dans les Andes.

Modélisation de l’invasion par la teigne de la pomme de terre dans les Andes tropicales

La présente étude a pour objectif la modélisation de ravageurs invasifs de la pomme de terre dans la région Nord andine. Le complexe d’espèces des teignes de la pomme de terre (TPT, Lepidoptera, Gelechiidae) représente une des principales menaces à la production de pomme de terre dans la zone tropicale et intertropicale. Trois espèces de ce complexe, *Phthorimaea operculella* (Zeller), *Symmetrischema tangolias* (Gyen) and *Tecia solanivora* (Povolny), ont envahi les paysages agricoles de la région nord-andine lors des 30 dernières années à partir d’introductions successives de différentes origines géographiques. Les larves des TPT creusent de profonds tunnels dans les tubercules de pomme de terre afin de se nourrir ce qui les rends impropres à la consommation et à la commercialisation. Les larves de *S. tangolias* and *P. operculella* peuvent aussi se nourrir des tiges et des feuilles des plants de pomme de terre. Les pertes de rendement causées par ces espèces sont considérables dans la région nord-andine, en particulier dans les régions les plus pauvres (Dangles et al. 2008). Plusieurs études ont montré que la température a une action prépondérante sur les dynamique des TPT (Keller 2003, Sporleder et al. 2004, Dangles et al. 2008) et représente donc un paramètre environnemental clé afin de générer des modèles régionaux de distribution et de propagation de ces espèces. De tels modèles représentent des outils intéressants afin d’améliorer le contrôle intégré de ces ravageurs car ils permettent l’élaboration de cartes de risques d’invasion et d’établissement à une échelle locale.

Afin de relever chacun des défis (précédemment mentionnés) concernant la modélisation de la dynamique spatio-temporelle de ces espèces, nous avons développé plusieurs stratégies, détaillées dans chacune des quatre parties de ce document de thèse, et résumées ci-dessous :

Chapitre 1 - Afin de mieux comprendre l’influence de l’hétérogénéité spatio-temporelle (induite par les activités humaines à l’échelle d’un paysage agricole) sur la propagation des teignes, nous avons développé un automate cellulaire simulant la dynamique d’invasion de *T. solanivora* dans une petite vallée des Andes, dans le centre de l’Équateur. Ce modèle nous a permis d’intégrer des informations détaillées concernant le paysage et de déterminer l’influence relative de l’hétérogénéité environnementale *versus* sociale sur la propagation des teignes. Nous avons ciblé notre étude sur deux types d’activité anthropique influençant la propagation des teignes : 1) la présence et la distribution de structures de stockage de tubercules qui modifient localement l'environnement thermique (Dangles et al. 2008, Appendix D), et 2) la dispersion passive à longue distance des teignes générée principalement par les échanges commerciaux et qui permet aux ravageurs de coloniser des zones en principe inatteignables par leurs propres capacités de dispersion (EPPO 2005, Dangles et al. 2010).

Chapitre 2 - Nous avons ensuite cherché à mieux comprendre le rôle de l'hétérogénéité environnemental des paysages tropicaux andins sur la dynamique des populations de teignes afin d'améliorer la fiabilité et la relevance de nos modèles (Gilchrist 1995, Davis et al. 2006, Adamo and Lovett 2011). Nous nous sommes principalement intéressés à comparer l'influence de températures constantes *versus* fluctuantes sur la dynamique d'oviposition des trois espèces de TPT. Dans ce contexte, nous avons développé un modèle de taux d'oviposition basé sur des données acquises à températures constantes, et l'avons utilisé afin de simuler des dynamiques populationnelles dans les cas de régimes thermiquement stables et fluctuants.

Chapitre 3 - Face à la disponibilité limitée de données empiriques et expérimentale nécessaires à la construction de modèles sur l'ensemble du gradient thermique dans lequel évoluent les teignes, nous avons évalué la robustesse de trois types de modèles de survie des TPT (Regnière, Sporleder et Sharpe et DeMichel) en présence de jeux de données limités, notamment aux limites de notre gradient thermique (températures minimales et maximales qui sont souvent les plus difficiles à obtenir). Nous avons ensuite confronté nos résultats à des données de terrain des limites de distribution altitudinales de nos trois espèces de teignes en Équateur.

Chapitre 4 – Enfin, nous avons construit un modèle individu centré permettant de simuler la survie, le développement et le taux d'oviposition des trois espèces de teignes en fonction de la température, en prenant en compte des générations successives d'individus soumis à différents régimes de températures journalières caractéristiques des Andes tropicales. Les sorties de ce modèle, couplé à la plateforme de modélisation BIOSIM, nous ont permis de construire des cartes de risques d'invasion de TPT à l'échelle de la région Nord-andine. Des scénarios de distribution spatiale de ces teignes dans le futur en fonction de plusieurs scénarios régionaux de changement climatiques ont aussi été établis à l'échelle de la zone nord-andine.

Mots clés

Automate cellulaire, changement climatique, espèces invasives, modèle individu centré, paysages agricoles, Région Nord Andine, teignes de la pomme de terre

References

Adamo, S. A., and M. M. E. Lovett. 2011. Some like it hot: the effects of climate change on reproduction, immune function and disease resistance in the cricket *Gryllus texensis*. Journal of Experimental Biology **214**:1997-2004.

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

Angilletta, M. J., R. B. Huey, and M. R. Frazier. 2010. Thermodynamic Effects on Organismal Performance: Is Hotter Better? Physiological and Biochemical Zoology **83**:197-206.

Angilletta, M. J., P. H. Niewiarowski, and C. A. Navas. 2002. The evolution of thermal physiology in ectotherms. Journal of Thermal Biology **27**:249-268.

Angilletta, M. J., T. D. Steury, and M. W. Sears. 2004. Temperature, growth rate, and body size in ectotherms: Fitting pieces of a life-history puzzle. Integrative and Comparative Biology **44**:498-509.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. Ecology **85**:1771-1789.

Buffoni, G., and S. Pasquali. 2010. Individual-based models for stage structured populations: formulation of "no regression" development equations. Journal of Mathematical Biology **60**:831-848.

Cadotte, M., S. McMahon, and T. Fukami. 2006. Conceptual ecology and invasion biology: reciprocal approaches to nature. Springer Verlag, Dordretch, The Netherlands.

Carrasco, L. R., J. D. Mumford, A. MacLeod, T. Harwood, G. Grabenweger, A. W. Leach, J. D. Knight, and R. H. A. Baker. 2010. Unveiling human-assisted dispersal mechanisms in invasive alien insects: Integration of spatial stochastic simulation and phenology models. Ecological Modelling **221**:2068-2075.

Dangles, O., C. Carpio, A. R. Barragan, J. L. Zeddam, and J. F. Silvain. 2008. Temperature as a key driver of ecological sorting among invasive pest species in the tropical Andes. Ecol Appl **18**:1795-1809.

Dangles, O., C. Carpio, M. Villares, F. Yumisaca, B. Liger, F. Rebaudo, and J. F. Silvain. 2010. Community-Based Participatory Research Helps Farmers and Scientists to Manage Invasive Pests in the Ecuadorian Andes. AMBIO. **39**:325-335.

Davis, J. A., E. B. Radcliffe, and D. W. Ragsdale. 2006. Effects of high and fluctuating temperatures on *Myzus persicae* (Hemiptera : Aphididae). Environmental Entomology **35**:1461-1468.

Denlinger, D. L. 1986. Dormancy in Tropical Insects. Annual Review of Entomology **31**:239-264.

EPPO. 2005. Data sheets on quarantined pests, *Tecia solanivora*. Bulletin OEPP/EPPO **35**:399-401.

Gilchrist, G. W. 1995. Specialists and Generalists in Changing Environments .1. Fitness Landscapes of Thermal Sensitivity. American Naturalist **146**:252-270.

Goslee, S. C., D. P. C. Peters, and K. G. Beck. 2006. Spatial prediction of invasion success across heterogeneous landscapes using an individual-based model. Biol Invasions **8**:193-200.

Grimbacher, P. S., and N. E. Stork. 2009. Seasonality of a Diverse Beetle Assemblage Inhabiting Lowland Tropical Rain Forest in Australia. Biotropica **41**:328-337.

Gutiérrez, J. A., J. D. Krenz, and N. R. Ibargüengoytía. 2010. Effect of altitude on thermal responses of *Liolaemus pictus argentinus* in Argentina. Journal of Thermal Biology **35**:332-337.

Harris, C. M., K. J. Park, R. Atkinson, C. Edwards, and J. M. J. Travis. 2009. Invasive species control: Incorporating demographic data and seed dispersal into a management model for *Rhododendron ponticum*. Ecol Inform **4**:226-233.

Herben, T., Z. Munzbergova, M. Milden, J. Ehrlen, S. A. O. Cousins, and O. Eriksson. 2006. Long-term spatial dynamics of Succisa pratensis in a changing rural landscape: linking dynamical modelling with historical maps. J Ecol **94**:131-143.

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

Huey, R. B., and R. D. Stevenson. 1979. Integrating thermal physiology and ecology of ectotherms: A discussion of approaches. American Zoologist **19**:357-366.

Jongejans, E., O. Skarpaas, and K. Shea. 2008. Dispersal, demography and spatial population models for conservation and control management. Perspect Plant Ecol Evol Syst. **9**:153-170.

Karl, I., S. A. Janowitz, and K. Fischer. 2008. Altitudinal life-history variation and thermal adaptation in the copper butterfly Lycaena tityrus. Oikos **117**:778-788.

Keller, S. 2003. Integrated Pest Management of the Potato Tuber Moth in Cropping Systems of Different Agroecological Zones. Margraf Publishers, Germany.

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

Messenger, P. S. 1959. Bioclimatic studies with Insects. Annual Review of Entomology **4**:183-206.

Nehrbass, N., E. Winkler, J. Mullerova, J. Pergl, P. Pysek, and I. Perglova. 2007. A simulation model of plant invasion: long-distance dispersal determines the pattern of spread. Biol Invasions **9**:383-395.

Opit, G. P., J. E. Throne, and M. E. Payton. 2010. Reproductive Parameters of the Parthenogenetic Psocid Lepinotus reticulatus (Psocoptera: Trogiidae) at Constant Temperatures. Environmental Entomology **39**:1004-1011.

Prasad, A., L. Iverson, M. Peters, J. Bossenbroek, S. Matthews, T. Davis Sydnor, and M. Schwartz. 2010. Modeling the invasive emerald ash borer risk of spread using a spatially explicit cellular model. Landscape Ecol **25**:353-369.

Régnière, J., V. Nealis, and K. Porter. 2009. Climate suitability and management of the gypsy moth invasion into Canada. Biol Invasions **11**:135-148.

Régnière, J., J. Powell, B. Bentz, and V. Nealis. submitted. Temperature Responses of Insects: Design of Experiments, Data Analysis and Modeling. Ecological Applications.

Savage, Van M., James F. Gillooly, James H. Brown, Geoffrey B. West, and Eric L. Charnov. 2004. Effects of Body Size and Temperature on Population Growth. The American Naturalist **163**:429-441.

Sebert-Cuvillier, E., V. Simon-Goyheneche, F. Paccaut, O. Chabrerie, O. Goubet, and G. Decocq. 2008. Spatial spread of an alien tree species in a heterogeneous forest landscape: a spatially realistic simulation model. Landscape Ecol **23**:787-801.

Soons, M. B., J. H. Messelink, E. Jongejans, and G. W. Heil. 2005. Habitat fragmentation reduces grassland connectivity for both short-distance and long-distance wind-dispersed forbs. J Ecol **93**:1214-1225.

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

Steigenga, M. J., and K. Fischer. 2009. Fitness consequences of variation in developmental temperature in a butterfly. Journal of Thermal Biology **34**:244-249.

Stiling, P. 2002. Ecology: Theories and Applications, 4th edition. Prentice-Hall, Inc., New Jersey.

Stillwell, R. C., and C. W. Fox. 2005. Complex Patterns of Phenotypic Plasticity: Interactive Effects of Temperature during Rearing and Oviposition. Ecology **86**:924-934.

Travis, J. M. J. 2010. Towards a mechanistic understanding of dispersal evolution in plants: conservation implications (vol 16, pg 690, 2010). Diversity and Distributions **16**:877-877.

Travis, J. M. J., C. M. Harris, K. J. Park, and J. M. Bullock. 2011. Improving prediction and management of range expansions by combining analytical and individual-based modelling approaches. Meth Ecology Evolution:Published online.

Vazquez, D. P., and R. D. Stevens. 2004. The latitudinal gradient in niche breadth: Concepts and evidence. American Naturalist **164**:E1-E19.

Venette, R. C., D. J. Kriticos, R. D. Magarey, F. H. Koch, R. H. A. Baker, S. P. Worner, N. N. G. Raboteaux, D. W. McKenney, E. J. Dobesberger, D. Yemshanov, P. J. De Barro, W. D. Hutchison, G. Fowler, T. M. Kalaris, and J. Pedlar. 2010. Pest Risk Maps for Invasive Alien Species: A Roadmap for Improvement. Bioscience **60**:349-362.

Vinatier, F., F. Lescourret, P. F. Duyck, O. Martin, R. Senoussi, and P. Tixier. 2011. Should I Stay or Should I Go? A Habitat-Dependent Dispersal Kernel Improves Prediction of Movement. Plos One **6**.

Young, K., and J. Lipton. 2006. Adaptive Governance and Climate Change in the Tropical Highlands of Western South America. Climatic Change **78**:63-102.

IRD, UR 072, Diversité, Ecologie et Evolution des Insectes Tropicaux, Laboratoire Evolution, Génomes et Spéciation, UPR 9034, CNRS, 91198 Gif-sur- Yvette Cedex, France and Université Paris-Sud 11, 91405 Orsay Cedex, France

Laboratorio de Entomología, Facultad de Ciencias Exactas y Naturales, Pontificia Universidad Católica del Ecuador, 12 de Octubre, 1076 y Roca, Quito, Ecuador

Centre d'Ecologie Fonctionnelle et Evolutive, Equipe BIOFLUX, CNRS, 1919 route de Mende, 34293 Montpellier cedex 5, France

TABLE OF CONTENTS

LIST OF PAPERS

1. **Crespo-Pérez V**, Silvain JF, Dangles O. Modeling invasive species spread in complex landscapes: the case of potato moth in Ecuador. Landscape Ecology (Accepted).
2. **Crespo-Pérez V**, Dangles O, Chuine I, Régnière J. Modeling insect oviposition in heterogeneous thermal environments: insights from potato tuber moth in the tropical Andes (Manuscript).
3. **Crespo-Pérez V**, Dangles O, Régnière J, Chuine I. Modeling temperature-dependent survival with small data sets: Insights from potato pests in the tropical Andes (Manuscript).
4. **Crespo-Pérez V**, Régnière J, Chuine I, Rebaudo F, Dangles O. Pest risk mapping in highly heterogeneous regions: The case of Potato Tuber Moth in the Tropical Andes (Manuscript).

Published papers (paper 1, published online 9/17/2011, and papers in Appendices 10, 11, 12 and 13) have been reprinted with kind permission from the copyright holders.

INTRODUCTION

1. INSECTS' LIFE CYCLE, DYNAMICS AND DISTRIBUTION

Organisms' physiology, behavior, abundance and distribution are highly influenced by their environment (Messenger 1959, Angilletta et al. 2010). Understanding the responses of organisms to environmental variables is a key element for simulating their dynamics in particular environments and consequently making predictions about their phenology and geographic distribution (Messenger 1959, Régnière 1996, Logan et al. 2007). Such forecasting capabilities are of prime importance for the fields of economic entomology, invasion biology, and pest ecology since they allow a more accurate timing and placement of pest management efforts (Régnière and Sharov 1998).

As pointed out by Andrewartha and Birch (1960), an animal's environment comprises four main components: weather, food, other organisms (of the same or of different species), and "a place in which to live" (i.e. the habitat). Even though, in theory, animals might be influenced by all of these components, in practice, only one or a few of these may account for most of the variability observed in life-history patterns and population dynamics (Andrewartha and Birch 1960). In the case of ectothermic organisms, such as insects, temperature is a key environmental factor. It has been shown to influence everything from temporal patterns of growth, survival, and reproduction (Angilletta et al. 2002, Savage et al. 2004, Stillwell and Fox 2005, Steigenga and Fischer 2009, Gutiérrez et al. 2010, Opit et al. 2010) to spatial patterns of body size, population density and species diversity and distribution (Angilletta et al. 2004, Brown et al. 2004, Hodkinson 2005, Karl et al. 2008, Régnière et al. 2009).

The importance of temperature in controlling ecological processes lies on its influence on biochemical reaction rates, metabolic rates, and nearly all other rates of biological activity (Hochochka and Somero 2000, Brown et al. 2004). Angilletta defines the thermal sensitivity as the degree to which an organism's performance depends on its temperature (Angilletta 2009). According to this same author there are three factors that cause thermal sensitivity at the cellular level: 1) thermal effects on enzymes and other proteins, where temperature changes alter enzymes' conformation and may impair their function; 2) effect of temperature on the movement and conformation of cellular membranes, where relatively low temperatures slow the movements of phospholipids resulting in a gel-like membrane whereas relatively high temperatures speed movements too much, disrupting the laminar structure of the membrane; 3) limitations on aerobic respiration posed by temperature, where low temperatures hamper mitochondrias from generating the ATP required for activity, and high temperatures cause ventilation and circulation to fall below the level to supply the mitochondria with sufficient oxygen.

The relative influence of the factors described above for insect life likely depends on the thermal environment where species live. For example, by summarizing global scale data collected from various groups of predominantly marine water breathing but also of air breathing ectotherms, Portner (2002) argued that oxygen limitation may be the most plausible determinant of organisms' thermal tolerances. However, Angilletta (2009) noted that this may not be true in heterogeneous environments where organisms can use anaerobic respiration to endure transient exposures to extremely high temperatures. Other studies, such as that of van der Have (2002) have shown that thermal limits on enzymatic activity can explain the thermal limits on embryonic and larval development of ectotherms. However, as stated by Angilletta (2009) determining the contribution of each factor to thermal sensitivity is difficult since thermal limits are probably the result of complex interactions at the biochemical, cellular and systemic levels. Despite such a complexity, there are two generalities that may be drawn from all these mechanisms: 1) there is a tradeoff between performance at high temperatures and performance at low temperatures, and 2) an increase in the performance breadth should cause a decrease in the maximal performance (this phenomenon is commonly referred to as a specialist-generalist tradeoff) (Huey and Hertz 1984, Gilchrist 1995, Angilletta 2009).

Thermal sensitivity at the cellular level leads to sensitivities at the systemic and organismal levels as well, restricting fitness enhancing activities to a narrow range of preferred temperatures (Gilchrist 1995). Knowledge about thermal sensitivity on whole-animal systems is ecologically more relevant than knowledge of the influence of temperature on cells or tissues. Understanding the influence of temperature on fitness allows analyses of geographic distribution, times of activity and competitive interactions of animals in relation to temperature (Huey and Stevenson 1979). Ecological modeling including organisms' level response to temperature is a common approach for analyzing such information.

2. MODELING INSECTS' ENVIRONMENTAL-RELATED PERFORMANCE

Starfield and Bleloch (1986) defined a model as "any abstraction or representation of a system or process." In ecology, models are simplified representations of nature that help us to simulate and understand observed ecological phenomena (Angilletta 2009). These tools are widely used by ecologists to simulate organisms' responses to environmental conditions (for a review see Worner 1991). Ideally, models should be built in the basis of previous observations and should be able to predict unobserved phenomena. When modeling the influence of the environment on organisms' responses, the common approach is to fit functions or curves to observed data of responses in relation to some environmental gradient (Huey and Stevenson 1979). This allows subsequent estimation of responses under actual or theoretical conditions. Integrating several models explaining related mechanisms into a larger one allows the simulation of more complex phenomena (Angilletta 2009). For instance one may be able to simulate the life-history, phenology, population dynamics or distribution of a group of organisms across time under varying environmental conditions (Buffoni and Pasquali 2010). Constant improvement of computational capacities allow increasing the complexity of models and running them at larger scales of time and space (Logan et al. 2007, Régnière et al. submitted).

2.1. Past, present and future of performance models

The effects of environmental factors on insects have long interested scientists (Sanderson and Peairs 1913, Peairs 1914, Alpatov and Pearl 1929, Uvarov 1931, Janisch 1932, Talbot 1934, Dennis 1938, Cloudsley-Thompson 1956). Early investigations were mostly descriptive and fragmentary and did not allow developing generalizations (Sanderson and Peairs 1913, Uvarov 1931). In 1931, Uvarov wrote a monograph summarizing existing work on the influence of climate on insects (see reviews in Cook 1932 and Russel 1933). Uvarov recognized the complexity of studying the influence of climate on insects and maintained that it should forcefully rely on analytical methods. This author also stated that the influence of each climatic factor on each phase of an insect's life should be studied independently. From that time on, a lot of work has been done concerning the climatic niche of insects. Much of this work has focused exclusively on temperature since it is recognized as the most important variable shaping insects' life (Janisch 1932, Powsner 1935, Davidson 1944, Messenger and Flitters 1958, Butler et al. 1976, Sharpe and DeMichele 1977, Schoolfield et al. 1981, Worner

1992, Gilbert et al. 2004, Walters and Hassall 2006, Steigenga and Fischer 2007, Abril et al. 2010).

Organisms' responses to environmental variables are commonly depicted with performance curves (Huey and Kingsolver 1989, Gilchrist 1995, Martin and Huey 2008, Angilletta 2009) which describe performance along a continuous environmental gradient. Angilletta (2009) defines performance as "any measure of an organism's capacity to function, usually expressed as a rate or probability." In the case of responses to temperature, these curves are commonly referred to as thermal performance curves. They share certain important properties like a unimodal shape, a negative skew and a finite breadth, and are commonly described with several parameters (Fig 1): 1) optimum temperature (T_{opt}), or optimum temperature range, which corresponds to the temperature, or range of temperatures, that maximizes performance; 2) thermal breadth (T_{br}) or performance breadth; 3) thermal limits which represent the minimum and maximum temperatures at which performance is greater than zero (T_{min} and T_{max}, respectively), and the maximal performance (P_{max}) which defines the level of performance at the optimum temperature (Huey and Stevenson 1979, Huey and Kingsolver 1989, Gilchrist 1995, Angilletta 2009, Angilletta et al. 2010).

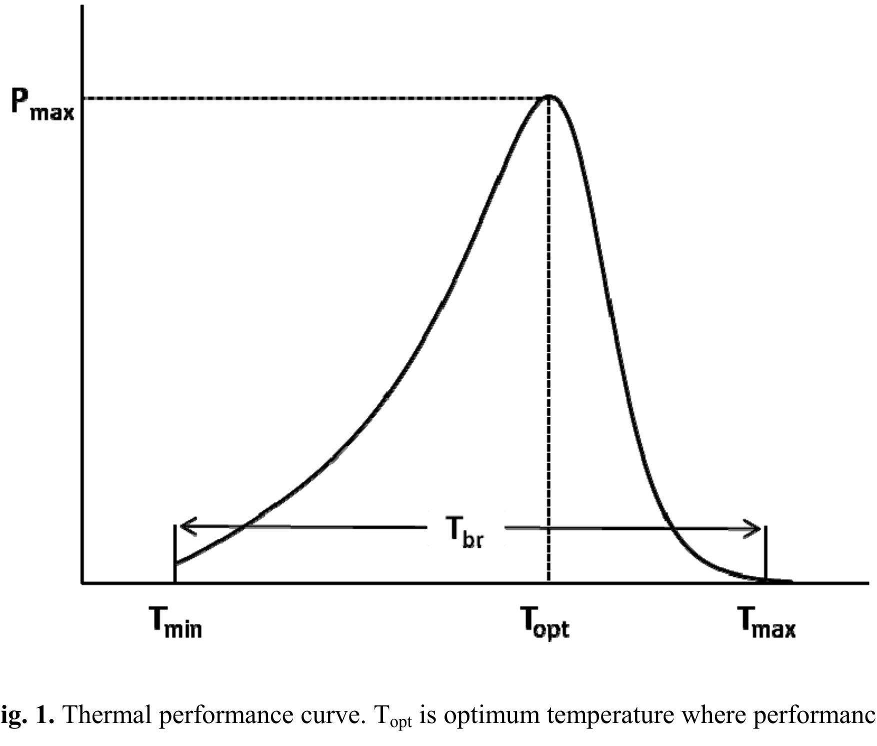


Fig. 1. Thermal performance curve. T_{opt} is optimum temperature where performance is maximized, T_{min} and T_{max} are minimum and maximum temperatures at which performance is greater than zero, T_{br} is thermal breath and P_{max} is maximal performance at the optimum temperature.

The most common measures of thermal performance are survival, development, growth, fecundity, locomotion, assimilation, and foraging (Gilchrist 1995, Angilletta 2009). All these variables respond rapidly (and usually reversibly) to changes in temperature (Angilletta 2009). Performance curves of the different measures differ from each other in their thermal optimum, breadth and limits of performance. More importantly, each measure contributes to fitness in a different way (for instance, survival contributes geometrically whereas development contributes additively) causing patterns of variation along thermal clines to differ slightly among the different measures of performance (Lynch and Gabriel 1987, Gilchrist 1995, Angilletta 2009). A common approach to characterize thermal performance consists in relating temperature to performance with mathematical functions. Fitted functions to measures of temperature-related performance are known as performance models (Angilletta 2009). The different performance measures are usually described with different models and several different models, varying in complexity or biological significance may be used to describe the same performance measure (Bentz et al. 1991, Bonato et al. 2007, Zahiri et al. 2010). Here we will focus exclusively on survival, development, and fecundity, since those are the three performance measures considered in the rest of this study.

2.1.1. Survival

Observations of survival along temperature gradients usually present an inverted U shape, with low survival at high and low temperatures (van der Have 2002). The mechanisms causing thermal limits are most likely tied to enzymatic activity. Traditionally, mechanisms hampering survival at high temperatures were assumed to differ from those hampering survival at low temperatures. The former were thought to be related to irreversible denaturation of proteins and death, and the latter to zero activity of proteins by inactivation (Hochachka and Somero 1984). Work by van der Have (2002) suggested that both high and low thermal limits may be caused by inactivation of cell cycle proteins and that the inhibiting effect is symmetrical at the two temperature extremes.

Many researchers have documented the relationship between temperature and survival of ectotherms (see Angilleta et al. 2004 for a review). While some studies remain purely descriptive (Drent 2002, Abril et al. 2010), many have focused exclusively on thermal limits (Berrigan 2000, Hercus et al. 2000, Stillman and Somero 2000, Carrillo et al. 2005, Bahrndorff et al. 2009), and only a few have adjusted models to survival data (Perez-Mendoza et al. 2004, Sporleder et al. 2004, Bonato et al. 2007). Régnière et al. (submitted) developed a model of survival that integrates both the effect of temperature on survival (a parabolic function), and the temperature dependent developmental time (see Chapter 2).

Population models require simulating insects' dynamics over one or more generations. Thus one must be able to model survival over time, under varying temperature conditions. Since, as stated before, survival contributes geometrically to an organism's total fitness (i.e. total fitness is the product of survival at all time intervals) one may calculate an individual or a group's total life-time survival by multiplying survival probabilities during all time-steps (Lynch and Gabriel 1987, Angilletta 2009, Régnière et al. submitted)

2.1.2. Development

As the other performance measures, insect development occurs within a definite temperature range, with a lower threshold temperature – near which development asymptotically approaches zero (because insects often survive for long periods at cold temperatures with little or no development; e.g. during diapause) – and an optimum one of fastest development above which it declines abruptly to a lethal maximum temperature (Wagner et al. 1984). In the mid region of the temperature range a linear response occurs. From a biochemical point of view development process is a complex series of reactions involving numerous enzyme systems (Sharpe and DeMichele 1977). These enzymes are inactivated by extremely low or high temperatures and their reaction rates are temperature dependent and determine the rate of development of an organism. These responses may explain the observed form of temperature dependent development rates (Sharpe and DeMichele 1977).

Earlier approaches to model development considered only the linear portion of the curve to predict insect development times. This approach, known as a degree day model, is based on the work of several authors (Candolle 1855, Sanderson and Peairs 1913, Arnold 1960) and calculates the duration of development by adding up the number of thermal units (degree-hours or days) above the lower threshold temperature until these accumulate to a specific total (Wang 1960). Although still widely used due to the simplicity to parameterize, and minimal data requirement for formulation, these types of models are only valid if temperatures do not fall outside the linear region of the organism's thermal response (Wang 1960, Régnière and Logan 2003). Moreover, the threshold temperatures are often determined by extrapolating the straight line to the temperature axis, which causes the number of degree-days required for complete development to be too low at temperatures near the lower threshold and too high at or above the optimum (Wagner et al. 1984).

The inadequacy of degree day models has long been recognized, and several authors have developed or used alternative approaches to model ectotherm development. For instance, Belehradek (1935, cited in Wagner et al. 1984) developed an exponential equation that became linear on a log scale. This model was used by Drooz and Shreuder (1972) to describe Elm spanworm (*Ennomos subsignarius*, Hübner) temperature related eclosion, but did a poor job at simulating response at extreme temperatures. Janisch's (1932) model combined two exponential curves, the reciprocals of which describe the accelerating phase of development rate up to the optimal temperature and the decelerating phase beyond the optimum. This model was used with various degrees of success but has been criticized for computational difficulties (Huffaker 1944, Messenger and Flitters 1958). Development and use of non-linear functions became extensive in the 1970's in response to the technological advances of computers (Stinner et al. 1975, Logan et al. 1976, Sharpe and DeMichele 1977) and a wide variety of functions have been developed ever since (Gilbert et al. 2004, Zahiri et al. 2010). Some models are more descriptive than others, and some even have parameters that can be interpreted biologically (Logan et al. 1976) or biophysically (Sharpe and DeMichele 1977, Schoolfield et al. 1981). All of these models aim at accurately describing the nonlinearity of development rates at temperature extremes and are required whenever simulations must cover temperatures over the full range of the developmental range function (Worner 1992, Régnière et al. submitted).

Describing development over time is often achieved with a rate-summation approach. This method assumes that the effect of temperature on development is additive and that time remains constant during small intervals of time. Thus development during a life-stage is calculated by adding (integrating) development rates over short time steps. Change of stage is assumed to occur when the sum attains the unity (Logan et al. 1976, Logan and Powell 2001, Régnière et al. submitted).

2.1.3 Fecundity

Insect reproduction is influenced by several factors including gonadal and nutritional status, mate availability, mating status, and female fecundity (Steigenga and Fischer 2007, Brent

2010). Of these, fecundity (total number of eggs laid per female during her whole life span) has been found to be influenced by temperature (Kim and Lee 2003). Exposure to extreme temperatures causes specific and irreversible damage to females' reproductive system like lethal injuries to oocytes and ovarian development (Rinehart et al. 2000, Hance et al. 2007, Renault 2011).

Temperature related fecundity has been shown to present a bell shaped curve and has been modeled using non-linear or polynomial functions (Hilbert and Logan 1983, Shaffer and Gold 1985, Allen et al. 1995, Sporleder et al. 2004, Bonato et al. 2007). However, for population models it might be useful not only to describe the relationship between this variable and temperature, but also the rate of oviposition over time. This may be modeled by cumulating the number of eggs laid by females each time interval until they exhaust their reproductive resources (Kim and Lee 2003, Régnière et al. submitted).

2.2. Choosing among potential performance models

As described above, numerous models may be adjusted to performance data. Choosing which one to use is however not an easy task. Some arguments to select a model may relate to its biological realism or practical application (Worner 1992). One may also discriminate models based on the amount of variation described by each one (i.e. choosing the one with the highest R^2). However, this last approach may lead us to choose a highly complex model that over-fits the data. A more elegant model selection method consists in the use of information theory (Angilletta 2006). Information criteria, such as the AIC (Akaike Information Criterion) or the BIC (Bayesian Information Criterion), rank candidate models based not only on their goodness of fit to the data, but also on their complexity (the number of parameters), thus avoiding the choice of excessively complex models (Schwarz 1978, Burnham and Anderson 2002).

2.3. Recent advances with performance models

One very important application of performance functions may be the construction of population models that simulate insect life-history events, phenology or distribution over time under varying environmental conditions. One example of such models are cohort-based models which have been used for a long time to simulate dynamics of cohorts of individuals (group of insects that enters a stage during the same simulation time-step) (Curry et al. 1978, Wagner et al. 1985, Régnière 1987, Logan 1988). In these models, cohorts age according to a rate summation equation (Logan 1988, Bentz et al. 1991, Logan and Powell 2001), and variability in developmental times is included by modeling development according to some probability distribution. Survival and oviposition of cohorts may also be included to simulate population dynamics over several cycles. The downside of cohort models is that in some cases the number of cohorts can become quite large, and, especially in unseasonal environments, where organisms present multiple overlapping generations, the juxtaposition of cohorts may become difficult to manage. Moreover, because individual traits are not distinguished, they are not as easily amenable to modeling evolutionary adaptation (Régnière et al. submitted).

Advances in computational power have allowed the development of individual-based models (IBM) which simulate the influence of environment temporal variability on the development, survival and oviposition of a collection of individuals (Buffoni and Pasquali 2010). Each newly created individual is assigned its own traits, which allows it to go through successive life-stages at its own individual pace (Choi et al. 2006, Willis et al. 2006, Nehrbass and Winkler 2007). For example, individuals may be randomly assigned different values of deviation from mean development time for each life stage, according to some distribution, or females may be assigned some initial fecundity at random. Régnière et al. (submitted) propose modeling survival by drawing a number from a uniform probability and removing the individual if the number is larger than its survival probability during that time step. In spite of their high computational demands IBMs are becoming quite popular since they allow modeling complex behaviors, including natural selection by simulating transmission of traits from parent to progeny (Régnière et al. submitted). Such an approach would allow understanding and predicting the evolution of thermal performance curves, which would greatly contribute to the progress of evolutionary thermal biology (Angilletta 2009). Furthermore, mounting evidence of genetic changes in response to recent, rapid climate change (Bradshaw and Holzapfel 2006, Kearney et al. 2009) emphasizes the importance of simulating the evolution of climate-related traits. This is especially the case for insects which have been shown to evolve faster than other groups (Bradshaw and Holzapfel 2006).

Population models driven by climatic variables such as cohort models or IBMs are powerful tools for simulating insect life-history over wide spatial and temperature scales.

These models allow assessing the level of success of populations across a landscape, and anticipating extinctions or eruptive population behaviors that may have strong impacts on the natural or agricultural landscapes where populations reside. These tools are becoming a popular component of pest-risk assessments both under current climatic conditions or under climate change scenarios (Jarvis and Baker 2001, Venette and Gould 2006, Logan et al. 2007, Venette et al. 2010).

Even though the necessary tools for successfully modeling insect's population dynamics and distribution seem to be ample and readily available, work on this subject in the tropics has lagged behind that of other regions. Given the vulnerability of tropical regions to many environmental threats related to our thematic, such as climate change (Bradley et al. 2006), increased frequency of extreme climatic events (IPCC 2007), and increasing occurrence of invasive insects (Nwilene et al. 2008), current research should focus its efforts on improving the knowledge about insect life in these regions and developing models that allow understanding and anticipating the risks associated with them.

2.4. Merging performance and spatially-explicit models

The spatial component of species dynamics (e.g., dispersal, site-specific conditions) is of prime importance for management aimed at controlling or conserving species (Jongejans et al. 2008). Spatial population models integrate information about species' demography and dispersal allowing predictions to be made not only about the rate but also the direction of spread (Jongejans et al. 2008, Cacho et al. 2010). There is a wide range of spatial population models, with varying levels of detail both in population dynamics – some models simulate dynamics in an unstructured way (Skarpaas and Shea 2007) while others specify age- or stage-structure (Neubert and Caswell 2000, Hunter and Caswell 2005) – and in spatial structure – some models consider an homogeneous landscape (Travis et al. 2011) whereas others simulate dynamics in a heterogeneous space (Moilanen 1999, Hanski et al. 2000, Herben et al. 2006, Carrasco et al. 2010).

Many organisms experience a world that is heterogeneous and patchy, and their population dynamics may be strongly influenced by such heterogeneity (Cadotte et al. 2006, Jongejans et al. 2008). Simulating spread in those types of landscapes or regions thus greatly benefits from realistic inclusion of spatial structure (Sebert-Cuvillier et al. 2008, Vinatier et al. 2011). Numerous types of models simulate space explicitly. These include patch-based metapopulation 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, Vinatier et al. 2009, Travis et al. 2011), and cellular automata (CA) models (Soons et al. 2005, Herben et al. 2006, Prasad et al. 2010). CA models can simulate space with the use of geographic maps, making them not only spatially explicit, but spatially realistic (Harris et al. 2009). These are of particular use when one is interested in understanding species' dynamics in landscapes with a particular configuration (Jongejans et al. 2008). Both CA and IBM models are able to incorporate demographic complexity although the latter in much more detail since they contain information about each individual in the population (Nehrbass et al. 2007, Jongejans et al. 2008). These two types of models are of great use to simulate and understand population and spread dynamics in highly variable regions like the Tropical Andes where dynamics are not only influenced by environmental heterogeneity but also by socially- induced heterogeneity.

3. INSECT DISTRIBUTION MODELING IN TROPICAL HIGH ALTITUDE LANDSCAPES

3.1. What are the challenges?

3.1.1. Assessing the influence of human impacts

Tropical regions lie between 20° N and 20° S of latitude. Despite the great diversity of environments among them, tropical high altitude regions share attributes that distinguish them from those of temperate zones. Among them, unlike high altitude landscapes in temperate regions, which are commonly regarded as relatively pristine places, tropical mountains have a long history of human occupation and impact. Andean landscapes, for example, have supported millions of people and vigorous societies throughout millennia (Young 2009). They have thus been exposed for a long time to chronic anthropogenic disturbances from fires, firewood harvesting, grazing, and cutting to establish agricultural plots (Young and Lipton 2006, Nyssen et al. 2009). Human impacts cause dramatic changes in tropical mountains.

Seeking short-term increase in agricultural production, farmers tend to augment pressure on the land, for example through reduced fallowing, removal of vegetation between cropland, and conversion of forest and woodlands on steep slopes into rangeland and marginal arable land (Nyssen et al. 2009). These impacts have further fragmented the inherently complex tropical mountains transforming them into composite mosaics of cultivated fields with different crops at several stages of maturation (Young and Lipton 2006, Dangles et al. 2008). The risk related to invasive pests in tropical mountains is higher, first because more species can be "packed" along altitudinal gradients and second, because increased commercial exchanges, with poor sanitary controls allow invasive species to propagate across cultivated landscapes (Dangles et al. 2010). Understanding and forecasting invasive distribution and spread is thus a timely issue in these landscapes that should forcefully account for the influence of anthropogenic impacts on species' dynamics.

3.1.2. Accounting for climatic heterogeneity

Climatic variability in tropical mountains strongly influences species dynamics and should be considered when modeling species distribution in these regions. Unlike temperate zones, seasonal variations in temperature are small (Denlinger 1986, Stiling 2002, Vazquez and Stevens 2004, Dangles et al. 2008, Angilletta 2009, Grimbacher and Stork 2009) and seasonal markers such as day length variation are absent. Therefore, population dynamics of organisms from tropical regions differ from those from temperate zones. For example, adaptations like temperature or day-length induced seasonality have not been observed in tropical species. Also, unlike temperate species, that usually synchronize their life-cycle events with seasonal cycles, tropical species commonly present several overlapping generations per year with no temperature-related synchronization in events like emergence or egg hatch (Denlinger 1986). Another important characteristic of these landscapes is the clinal decrease in air temperature related to increase in altitude (Stiling 2002, Angilletta 2009). This contributes to the high spatial heterogeneity characteristic of tropical mountains and causes thermal limits and population dynamics of species to be defined spatially rather than seasonally (Dangles et al. 2008). Another important feature of tropical mountains is that daily variations in temperature are usually pronounced and are often much greater than yearly variation in mean monthly temperature (Denlinger 1986). The thermal environment experienced by insects in these regions is therefore one of strong temperature fluctuations. Knowledge about insect responses to this type of temperature regime is thus important for more robust and realistic predictions of their dynamics.

3.1.3. Working with scarce data

A very important characteristic shared by tropical regions, which hinders development of distribution models, is that the majority of countries located in them are developing countries (see Dangles et al. 2009a). Due to less developed scientific research information concerning insects' responses to their environment is scarce and many times incomplete. Many studies reporting on experiments remain descriptive and lack necessary information such as sample numbers or standard deviations (Gamboa and Notz 1990, Notz 1995, Torres et al. 1997). Much of the existing information has not been published and has remained as "gray" literature, virtually unavailable for researchers in need of such information. The low number of weather stations in tropical regions causes climatic data to be scarce. Given the high topographic heterogeneity of tropical mountains, accurate weather interpolation to whole regions may be difficult. This lack of weather data also increases the already high uncertainty of climate change predictions (Buytaert et al. 2010). Additionally, information regarding land-use and land-use changes is usually outdated and existing maps usually have a very low resolution. Finally, data on presence and absence of pests, necessary to evaluate model predictions is commonly lacking. All this demands great effort for modelers either to find existing information or to develop it themselves in order to construct adequate models and the subsequent validation of model outputs.

3.1.4. Building distribution maps under current and future climate

Distribution models are commonly used to build pest risk maps which describe the probability of pests invading or establishing across a region or landscape (Venette et al. 2010). Building these maps at a regional scale in tropical mountains is usually faced with all or some of the abovementioned challenges. Realistic forecasting of species presence, for example, should account for the high heterogeneity of these regions, both temporally and spatially. Information needed to build these maps includes data about species responses to the environment, detailed information about climatic variability and actual pest distribution (Jarvis and Baker 2001, Logan et al. 2007). Due to the high heterogeneity of mountain regions, the possible adaptation of populations to different environmental conditions and the changes in genetic diversity of invasive species (Torres et al. 1997, Sakai et al. 2001) distribution models should ideally be parameterized with data from several populations from different geographic locations.

Climatic changes are predicted to increase in the future, supposedly to a greater extent in mountainous regions (Still et al. 1999, Bradley et al. 2006, Urrutia and Vuille 2009, Buytaert et al. 2010). Therefore, adaptation to future threats posed by pests must include predictions of future climate change. However, as mentioned above, uncertainties related to these types of predictions in regions where even actual weather data is scarce are even higher (Buytaert et al. 2010). Pest risk maps of future threats should thus consider several climate change scenarios and, ideally several climate change models.

4. MODELLING POTATO TUBER MOTH INVASION IN THE TROPICAL ANDES

The present study aimed at modeling the spread and distribution of three invasive species of Potato Tuber Moth (Lepidoptera, Gelechiidae) in the North Andean region. Bellow we discuss the general context that surrounds this study.

4.1. The Tropical Andes

The Tropical Andes are located in Northwestern South America and encompass an area of 2 033 000 km^2 (area over 1000 m.a.s.l., Nyssen et al. 2009) in the countries of Colombia, Ecuador, Peru and Bolivia (Plate 1). This region is characterized by strong environmental gradients mainly associated with changes in elevation (mountaintops can exceed 6000 m.a.s.l. with adjacent valley bottoms 3000–4000 m below) (Young and Lipton 2006, Young 2009). Spatial heterogeneity in the tropical Andes landscapes is indeed remarkable and is probably the most important feature shaping wildlife in this region (Young 1997).

Even though the Tropical Andes lack a clear seasonality in temperature, this region does present temporal variability in environmental conditions mainly related to variations in precipitation. This variation is caused by various factors, the most important of which is El Niño Southern Oscilation (ENSO) which causes annual or sometimes by-annual or even decadal oscillations causing increased rain or draught depending on the location (Young 2009, Poveda et al. 2011, Williams et al. 2011). Precipitation patterns may be further confounded by other mechanisms including 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). Precipitation patterns in the Tropical Andes are thus quite complex and difficult to predict and contribute to the high heterogeneity of the landscapes.

Like other tropical mountain regions, Tropical Andean landscapes have been intensely fragmented by long-term human influences, mainly related to agricultural practices (Young and Lipton 2006) that have transformed the region into a complex mosaic of cultivated fields (Plate 2). Agriculture is an important component of the economies of countries in the North Andean Region with many people depending directly or indirectly on agricultural activities (FAO 2011). Most farmers live in poverty and many are subsistence oriented with median to small farms (Plate 3). Productivity in the Tropical Andes faces many challenges associated with climate change and extreme events, limited access to technology and infrastructure (related to both elevated costs and remoteness of many sites), the low margins of gains related to the scale of operation, low levels of people's education, and socio-economic and institutional changes that have increased the pressure on natural resources, weakened the internal social organization and caused cultural erosion in the Andean society (Perez et al. 2010).

The emergence and propagation of agricultural pests constitute important threats to agriculture in the region. Losses caused by them are estimated to approach 60-70 % in available crop production and storage in developing countries (Nwilene et al. 2008). Climate change is believed to increase the risk related to pest species in the North Andes for at least two reasons. First, as stated before, temperature increase is expected to be greater in mountainous regions than in lowlands (Hodkinson 2005), and the long thermal gradients along mountains will potentially allow the persistence of microclimatic refuges that will eventually permit the presence of a higher number of pest species along the elevation gradient (Bale et al. 2002, Hagen et al. 2007, Dangles et al. 2008). Second, climate change will likely have indirect effects on the distribution of pest species through the upward shift in the agricultural frontier (Sarmiento 2002). Increase in temperature allows farmers to clear new land at higher altitudes to plant their crop, thus allowing pest species to also reach higher altitudes.

4.2. The Potato Tuber Moth complex

After cereals, potato is the most important food in the world. Potatoes have high nutritional values producing more usable energy than any other crop per space and time unit. Once boiled a medium sized potato provides half of the daily recommended values of vitamin C for an adult, as well as important quantities of iron, potassium, zinc, vitamin B and many essential microelements. It is therefore not surprising that potato is considered an extremely valuable tool in the fight against world hunger (Devaux et al. 2010).

Potatoes are produced in almost every country and each year more than 300 million metric tons are produced. Only a third of this production comes from developing countries, where potatoes are mainly grown on subsistence smallholdings (Radcliffe 1982, Keller 2003). In Tropical South America potatoes are grown in the Andes where they constitute central elements of household and national economies, contributing with more than 7 % of the countries' Gross Domestic Product (GDP) (Devaux et al. 2010). Also, potato is a very important source of employment and salary in the region with more than 820,000 producers in Ecuador, Peru and Bolivia. Although being the center of origin of potatoes, the tropical Andes contribute with only 1.38 % of world production. Lately, production has increased in this region, but yield is still considerably lower than the world average. Farmers face constant problems with potato production, some of them related to climate (such as frost, hail or draught) or economics of potato production, but mostly to pests and diseases which have been estimated to cause losses in production of 32% (Pumisacho and Sherwood 2002, Keller 2003).

The potato tuber moth (PTM) complex (Lepidoptera, Gelechiidae) represents one of the most important threats to potato production in tropical and subtropical regions. Three species of this complex *Phthorimaea operculella* (Zeller), *Symmetrischema tangolias* (Gyen) and *Tecia solanivora* (Povolny) (Plate 4), have been invading agricultural landscapes of the North Andean region within the last 30 years through successive introductions from different origins. Losses in yield caused by these species in the potato fields of the North Andes are considerable, especially in the poorest regions (Dangles et al. 2008).

P. operculella is thought to have originated in the tropical mountainous regions of South America and is now a cosmopolitan pest that can be found in almost all potato production areas worldwide (Radcliffe 1982, Rondon 2010). It is considered to be the most damaging insect pest of potato in the developing world (Keller 2003). *S. tangolias* originated in the Andes of Peru and Bolivia and has been moving north to Ecuador, where it was first reported in 2001. *T. solanivora* is native to Guatemala and the southernmost part of Mexico. It has been successively introduced into Cost Rica, Venezuela, Colombia and Ecuador, where it arrived in 1996 (Puillandre et al. 2008, Torres-Leguizamon et al. 2011). In South America, Ecuador is the southernmost limit of distribution of this species that has apparently been unable to invade potato fields of Peru.

PTM females lay their eggs on rough surfaces such as soil, potato tuber eyes, or leaf undersurfaces. After hatch, larvae dig into the soil until the find a potato tuber where they burrow deep tunnels in order to feed (Plate 5). *S. tangolias* and *P. operculella* larvae can also feed on stems and leaves of potato plants. When fully grown, larvae leave their host and pupate in the soil near the bases of plants, in leaf remains, near stored potatoes, or in other suitably sheltered sites (see Plate 6 for a graphic description of PTM life-cycle). The co-occurrence of the three species in the same potato field, sac, or potato storage structure has been observed only in Southern Colombia and Ecuador (Dangles et al. 2008). Information on the interaction of the three species is scarce. A recent study by Dangles et al. (2009b) found that damage to the crop was greater when the three species were present than that predicted from the added effects of each pest alone, and that this produced significant increases in pupal biomass and fecundity. Additional experiments have shown either facilitation or competition between the three species, depending on which one is initially present and on the sequence of infestation (Mazoyer 2007).

Temperature has been shown to be the main driver of PTM dynamics (Keller 2003, Sporleder et al. 2004, Dangles et al. 2008). Climatic conditions of the northernmost part of the Tropical Andes (e.g. Ecuador) present very little seasonal variation. This allows potatoes to be grown all year round, and causes the agricultural landscape of the highlands to be made up of a mosaic of potato field at various stages of maturation. This permits PTM to survive and be active all year round since they have constant favorable conditions in terms of climate and food resource. In this part of the Tropical Andes PTM distribution and population dynamics are thus defined spatially rather than seasonally (Dangles et al. 2008). As one moves farther south to Peru and Bolivia, seasonality becomes slightly more marked with potato production sometimes limited to a few months each year (i.e. in Puno and Cusco in southern Peru, potato is cultivated between May and September, Devaux et al. 2010). In these more southern landscapes PTM distribution and dynamics are influenced by temperature, rainfall and by food availability. Nevertheless, temperature has been shown to be of prime importance for these insects' life-cycle dynamics and has been shown to produce accurate phenology models (Sporleder et al. 2004, Dangles et al. 2008).

PTM infestation is usually higher in traditional potato storage structures (tubers heaped under a basic shelter) where re-infestation occurs and frequently the entire stored potato stock is destroyed. These structures offer optimal conditions for moth development, such as protection from coldest temperatures and against rainfall (Keasar et al. 2005), and explain the survival of *P. operculella* in places with cold winters like Northwest U.S.A. or central Europe (Rondon 2010). These human constructions seem thus determinant for PTM survival and establishment even in places with unsuitable climate.

Efficient management of PTM in the North Andean region is in most cases inadequate due to limited access to technology and funding and low levels of people education. Furthermore, transfer of knowledge on integrated pest management is hampered by the high inaccessibility of some villages or potato fields. Andean farmers and IPM technicians are in urgent need of new tools to enhance their capacity to fight against these pests. Recent advances in empirical data analysis and modeling allow developing approaches to better understand and predict pest dynamics and the level of risk of the landscapes to their invasion and establishment. Transferring this information to technicians is of prime importance to strengthen the resilience of the whole region to pest problems; technicians have indeed a key role in transferring advances in scientific knowledge to farmers.

4.3. The INNOMIP project

This PhD work has been realized within the INNOMIP project (INNOvative approaches to Manage Insect Pest risks in changing Andes), led by the French Institute for Research and Development (IRD) in collaboration with the Entomology Laboratory of the Pontifical Catholic University of Ecuador (PUCE). This program was developed to improve the capacity of North Andean farmers to fight against PTM and other agricultural pests and is a joint effort between several institutions of Ecuador, Peru and Bolivia concerned with integrated pest management (see www.innomip.ird.fr for further details).

This work benefited from being part of such a project mainly through the availability of data. Such data was in some cases used to parameterize our models. For instance, long term temperature monitoring in the field and in potato storage structures with data-loggers

(HOBBO, temperature and humidity, Plate 7), allowed us to determine the level of temperature buffering inside potato storage structures, which was included as a human influence factor driving PTM dynamics in one of our models (see section 4.4.1). The INNOMIP project also established a monitoring program of PTM in Ecuador, Peru and Bolivia (Plate 8). Moths were monitored with pheromone traps at several sites along gradients of altitude from the lower level of potato crop up to the agricultural frontier. Individual collections were realized every three weeks for 3 years. Data issued from this monitoring were useful for validating our modeling outcomes.

4.4. PTM distribution modeling: overcoming the challenges

We faced the challenges described in section 3 when modeling PTM distribution. Several strategies were developed to overcome these difficulties and are described in 4 articles written during this PhD, which correspond to the four chapters of this dissertation:

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

As stated before, landscapes in the Tropical Andes have been severely fragmented by human activity. In order to better understand the influence of this human-induced heterogeneity we developed a spatially-explicit, cellular automata model that simulated the spatio-temporal dynamics of *T. solanivora*'s invasion into a small valley in central Ecuadorian Andes. We chose this species since we disposed of data about its propagation into the valley which allowed us to evaluate propagation predicted by our model. This model allowed us to include detailed information about the landscape and to determine the relative influence of environmental versus social landscape heterogeneity on moth propagation. We focused on two human practices that influence PTM propagation: 1) the presence and distribution of potato storage structures that modify local thermal environment (Dangles et al. 2008, Appendix D), and 2) passive long- distance dispersal (LDD) of moth in human vehicles that allow moth to attain far away sites, unreachable with their intrinsic flight capacity (EPPO 2005, Dangles et al. 2010). Even though with this model we exclusively simulated *T. solanivora*'s propagation it may be used for the other two PTM species or for any invasive species for which one has mechanistic understanding about its basic environmental-related dynamics (survival, development, fecundity).

2) Modeling insect oviposition in heterogeneous thermal environments: insights from potato tuber moth in the tropical Andes

Thermal heterogeneity of the tropical Andes may greatly influence PTM dynamics. It has been shown that insects respond differently if exposed to constant or fluctuating temperature regimes, and accounting for these different responses may be of great importance for enhancing accuracy and realism of pest dynamics models (Gilchrist 1995, Davis et al. 2006, Adamo and Lovett 2011). Oviposition is one of the main components of insects' fitness and population dynamics (Berger et al. 2008) and is highly influenced by temperature. In this PhD we were interested in understanding the influence of constant and fluctuating temperatures on the oviposition dynamics of the three species of PTM. For this, an oviposition rate model developed with data at constant temperatures was used to simulate dynamics under both constant and fluctuating temperature regimes. In addition, we ran our simulations under real temperature regimes measured in the field and in storage structures located at various altitudes. The aim of this was to compare the influence of higher (in the field) and lower (in storage structures) temperature variability on the oviposition of PTM.

3) Modeling temperature-dependent survival with small data sets: Insights from potato pests in the tropical Andes

As stated before limited or small data sets are common caveats for distribution modeling of many agricultural pests in tropical regions. Successfully simulating pests' temperature-related responses requires an accurate estimation of their dynamics, especially near threshold temperatures (Angilletta 2009). This is of particular importance in places, like the Tropical Andes, where temperatures usually approach lower lethal extremes. Models capable of simulating lethal effects of extreme temperatures, even when parameterized with limited data sets, seem thus of great importance for population modeling in those cases. In this PhD we compared the ability of three approaches to model PTM survival. We were particularly interested in assessing the behavior of the models given a small data set that did not cover the whole temperature range. Accurately representing the physiological limits of species may be of particular importance in places like the Tropical Andes (and probably in other tropical regions), where adequate pest management is urgent but data are scarce.

4) Pest risk mapping in highly heterogeneous regions: The case of Potato Tuber Moth in the Tropical Andes

Pest risk maps are extremely useful tools employed by management programs (Venette et al. 2010) and are urgently needed in the Tropical Andes to improve the capacity of farmers and stakeholders to fight the increased threat posed by agricultural pests. A common approach for building these types of maps is to use the outputs of phenology models to assess climatic suitability of the region for pest invasion and/or establishment (Jarvis and Baker 2001, Logan et al. 2007). In this study we constructed a model that simulated PTM temperature-related survival, development and oviposition rate through successive generations under daily temperature regimes. Outputs of this model were then used to evaluate the level of risk associated with PTM across the region. Constructing such maps at this large scale proved challenging for several reasons. First, accurate generation of daily temperature regimes through interpolation of weather station data was difficult due to the scarcity of stations and to high topographic heterogeneity. Also, we were not able to include human-induced heterogeneity into this model due to lack of data on a regional scale. As evidenced by the Cellular Automota model, such information is necessary for improving model predictions. Finally, the lack of temperature-response data from populations of PTM from several geographic regions did not allow our model to accurately simulate the distribution of the species in some parts of the region. This may be due to the fact that populations may be adapted to local weather conditions or that changes in genetic diversity (i.e. genetic bottle necks) may have caused changes in populations' responses to temperature (Puillandre et al. 2008, Torres-Leguizamon et al. 2011). All this suggests future lines of work regarding pest risk mapping in tropical regions that would improve the reliability of predictions. Since climate changes are predicted to intensify in the future in the high Tropical Andes (Bradley et al. 2006) we ran our model under several climate change scenarios. Such simulations allowed us to make predictions about the future risks related to PTM across the region and about the expected shifts in the distribution ranges of the three species.

PLATES

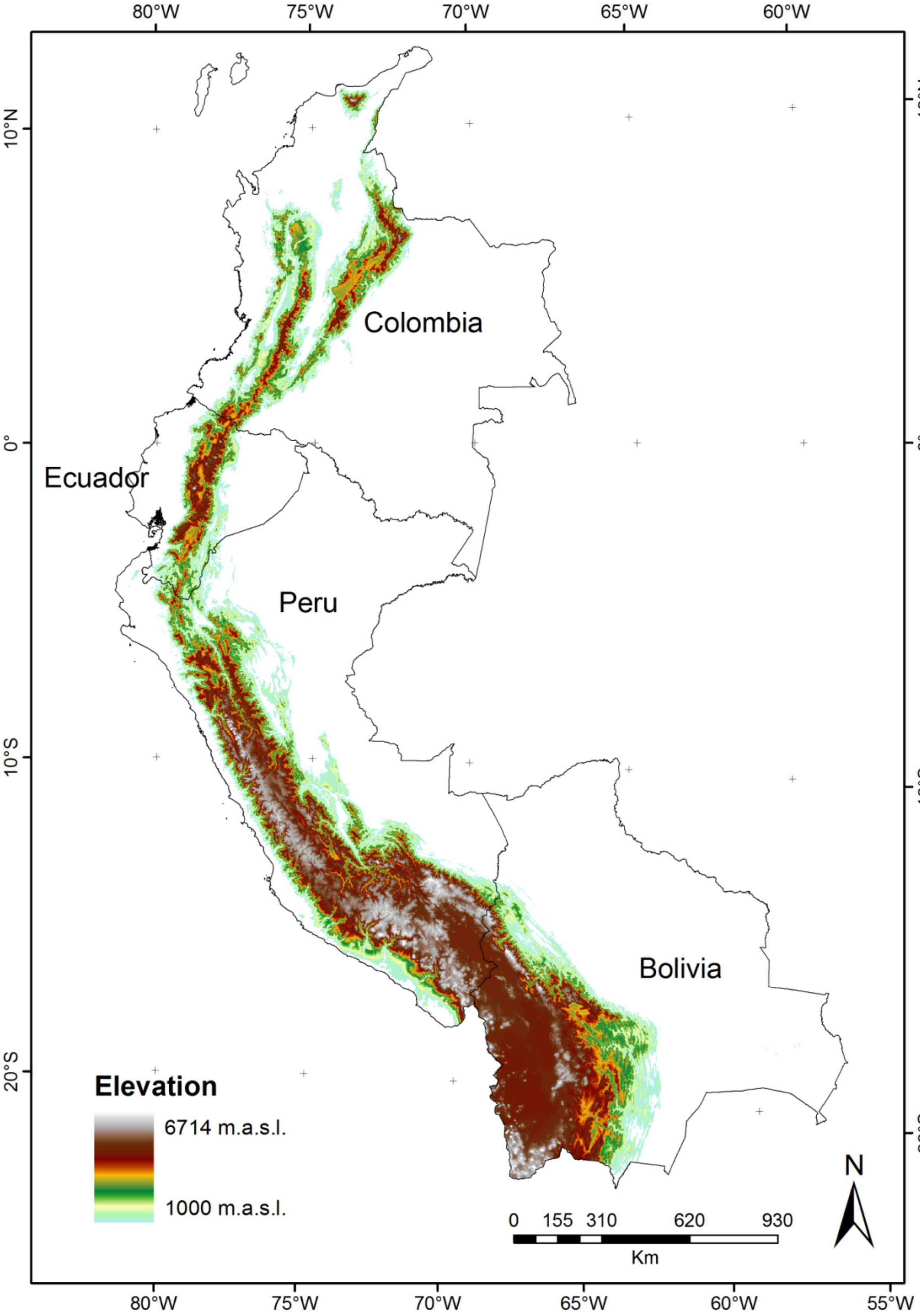


Plate 1. Map of the North Andean Region, showing zones 1000 m.a.s.l. which correspond to potato production zones.

Plate 2. Photograph of a cultivated landscape in the North Andes showing the complex mosaic of cultivated fields and sparse forests.

Plate 3. Farmers from a small valley in the Central Ecuadorian Andes during potato harvest.

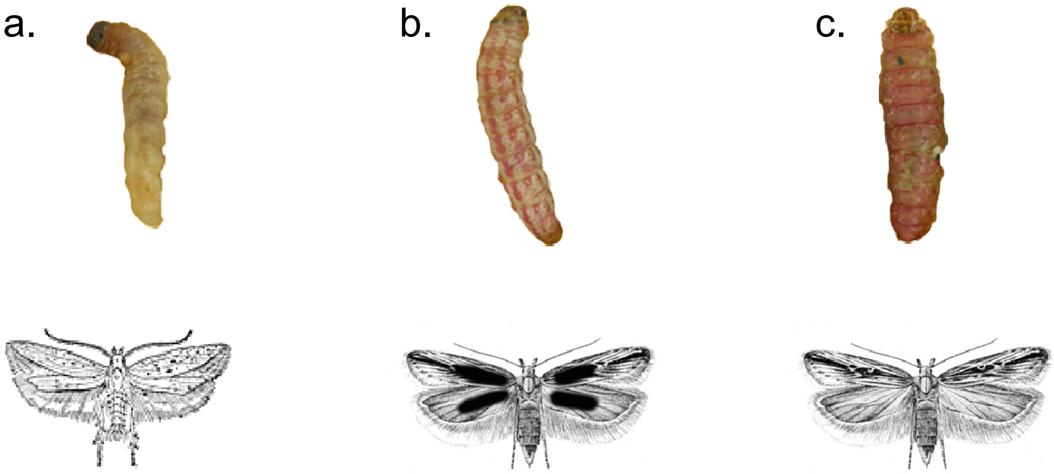


Plate 4. Larvae and adults of a) *Phthorimaea operculella*, b) *Symmetrischema tangolias* , and c) *Tecia solanivora*

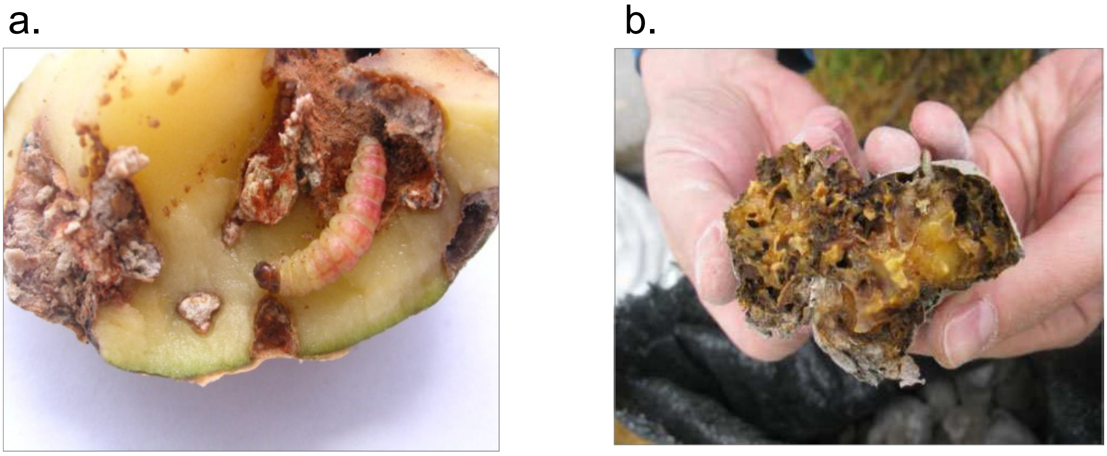


Plate 5. a) *T. solanivora* larva living inside a potato tuber, and damaged potato with galeries made by PTM larvae.

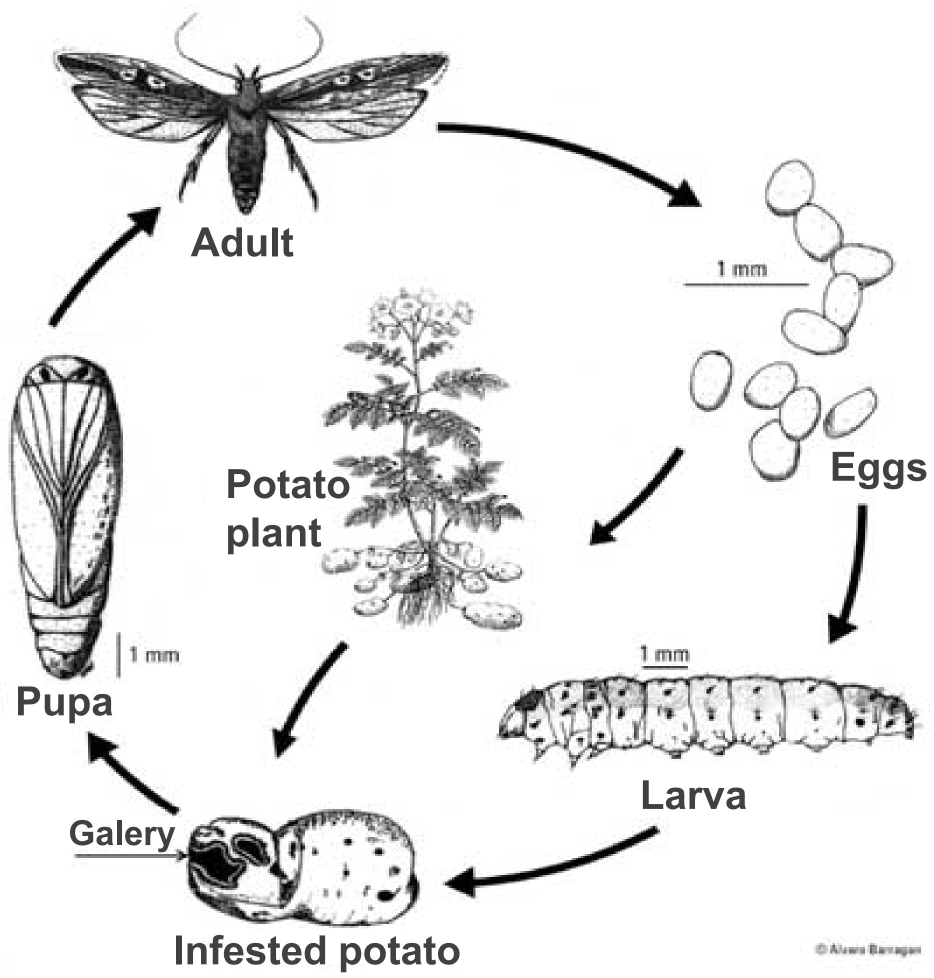


Plate 6. PTM life cycle

Plate 7. Temperature/humidity data-logger located next to a potato field in the Ecuadorian Andes.

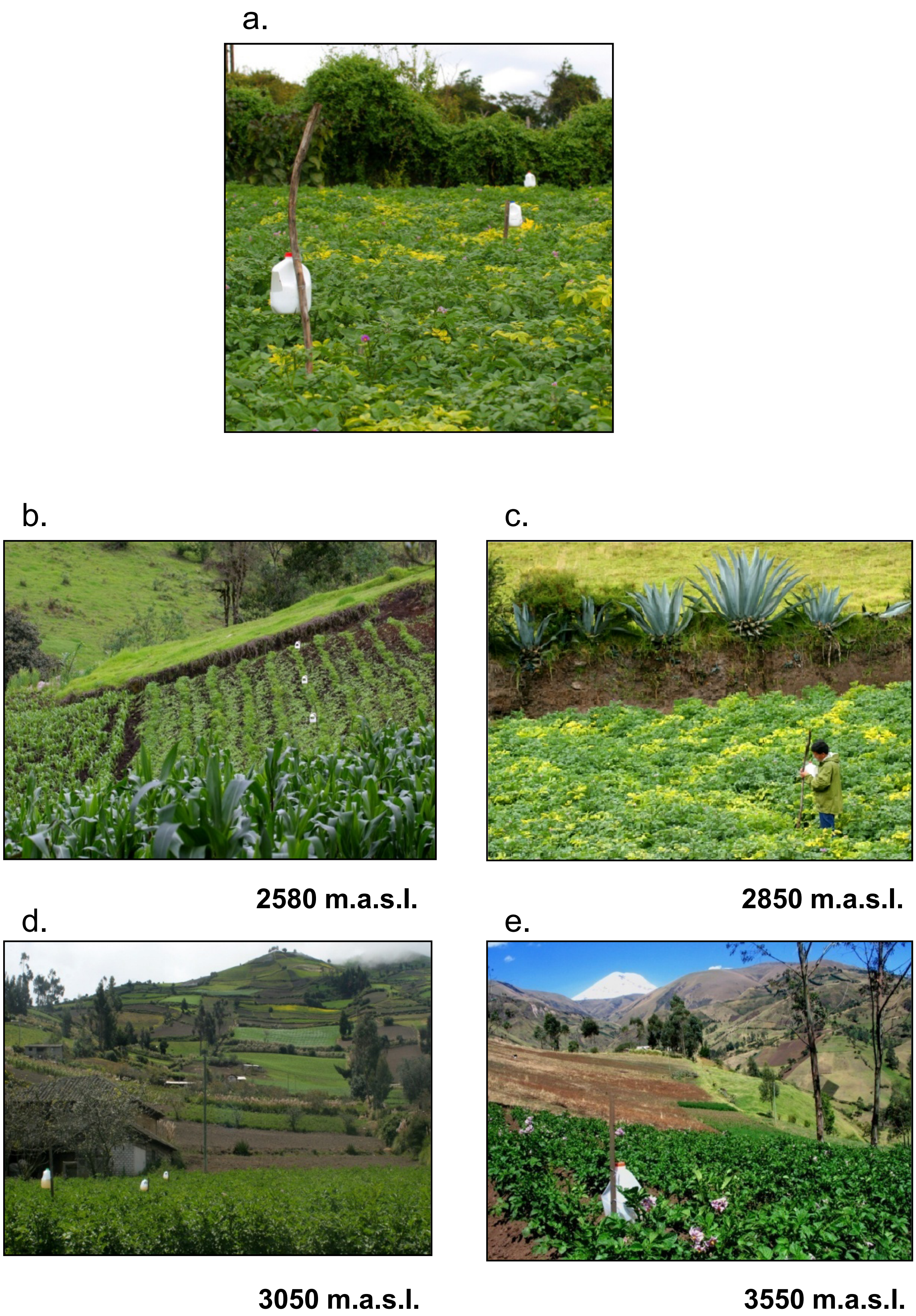


Plate 8. Moth monitoring at several sites in Central Ecuador along an altitudinal gradient. a) Shows the pheromone traps aligned in a potato fields. b-e show four different sites were monitoring was established.

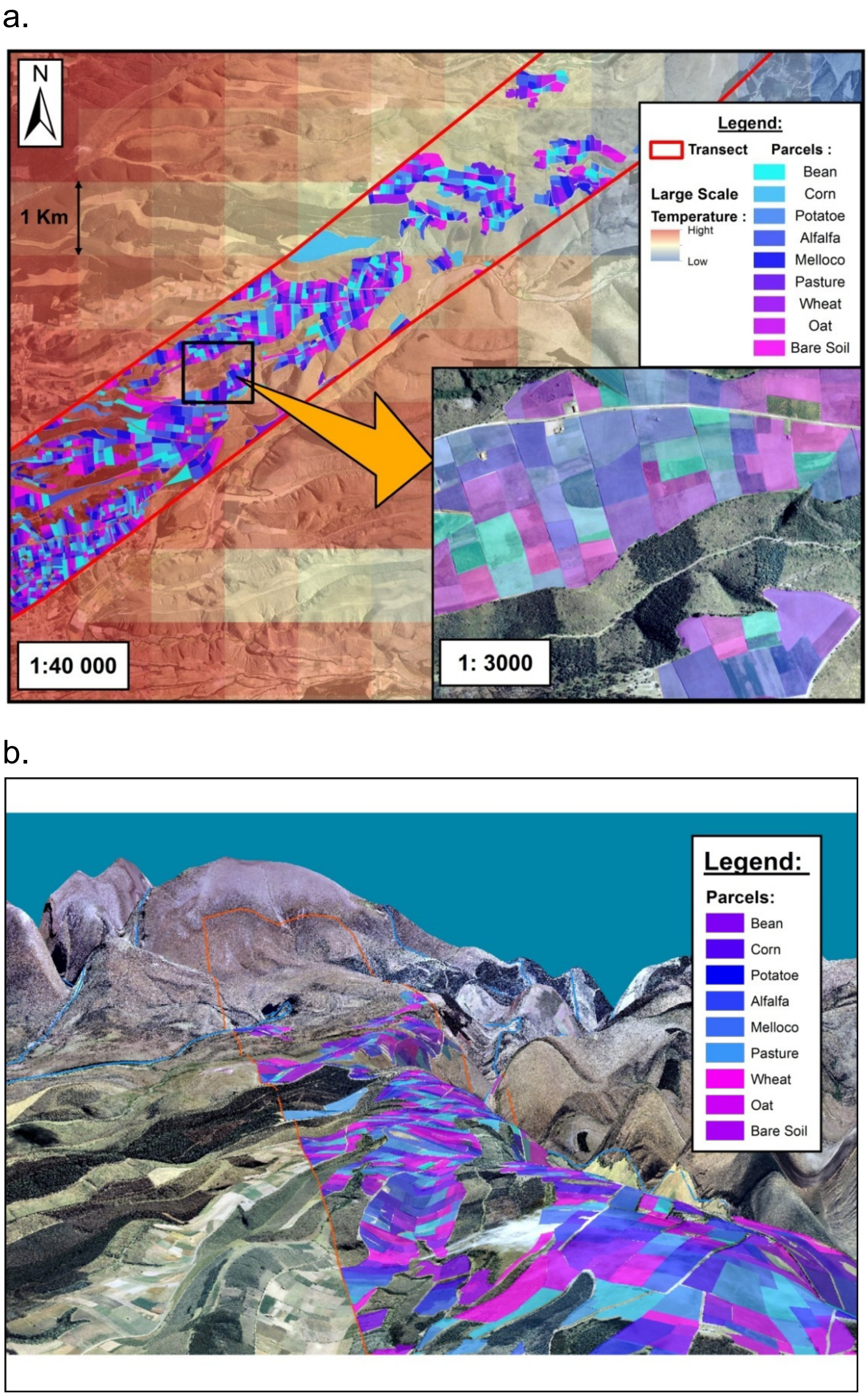


Plate 9. Agricultural landscape in the central Ecuadorian Andes. a) 2D view showing temperature variability across the landscape and the diversity of crop within a plot of 1 km^2. b) 3D view of the same landscape showing the high topographical heterogeneity of agricultural landscapes in the Ecuadorian Andes.

CHAPTER 1

Landscape Ecol
DOI 10.1007/s10980-011-9649-4

RESEARCH ARTICLE

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

Verónica Crespo-Pérez · François Rebaudo · Jean-François Silvain · Olivier Dangles

Received: 11 January 2011 / Accepted: 29 August 2011

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.

Keywords Boosted regression tree · Cellular automata · Crop storage structures · Gravity model · Invasive species · Long-distance dispersal · Mountainous landscapes · *Tecia solanivora* · Tropical Andes

---

Electronic supplementary material The online version of this article (doi:10.1007/s10980-011-9649-4) contains supplementary material, which is available to authorized users.

V. Crespo-Pérez · F. Rebaudo · J.-F. Silvain · O. Dangles
IRD, UR 072, Diversity, Ecology and Evolution of Tropical Insects Team, Evolution, Genomes and Speciation Laboratory, UPR 9034, CNRS, 91198 Gif-sur-Yvette Cedex, France

V. Crespo-Pérez · F. Rebaudo · J.-F. Silvain · O. Dangles
University Paris-Sud 11, 91405 Orsay Cedex, France

V. Crespo-Pérez (✉) · O. Dangles
Entomology Laboratory, Natural and Biological Sciences Faculty, Pontifical Catholic University of Ecuador, 1076 Av. 12 de Octubre and Roca St., Quito, Ecuador
e-mail: verocrespoperez@yahoo.com

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 metapopulation 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 km^2. 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.

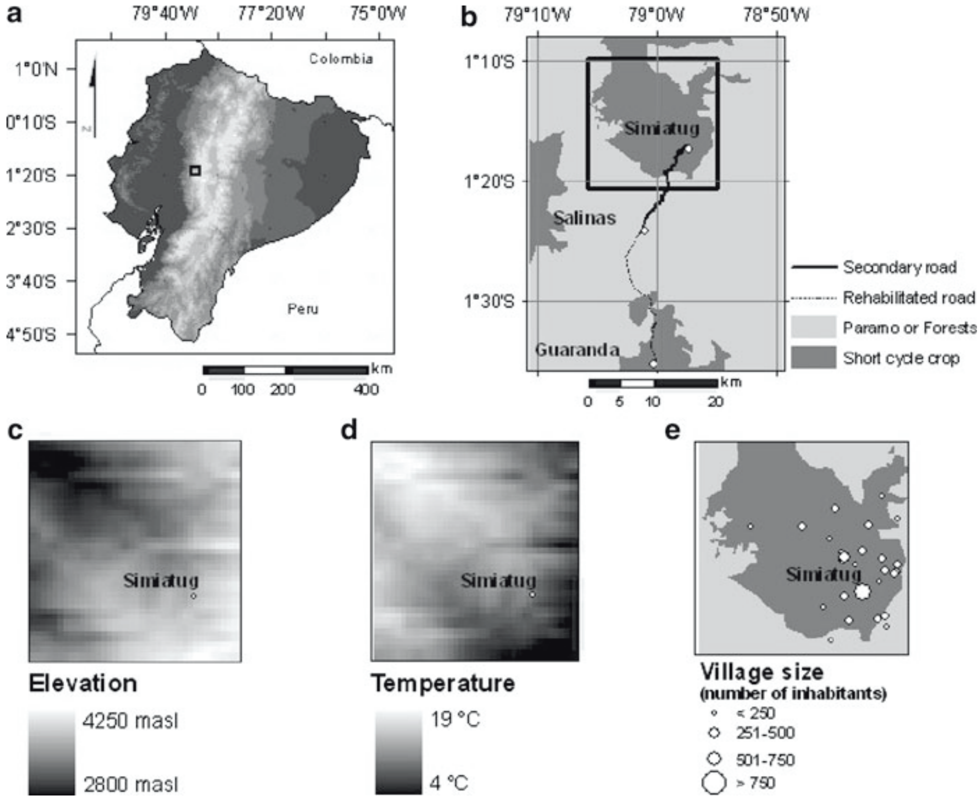


Fig. 1 Map of the study area showing **a** the location of the Simiatug Valley in the central Ecuadorian Andes; **b** land use in the area showing the specific area of 20 × 20 km of our cellular automaton (*black square*); **c** elevation of the cells of our grid; **d** mean yearly temperature of the 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:

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

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 ($P_{i\to j}$) as follows:

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

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 = 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:

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

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; Munkemuller 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).

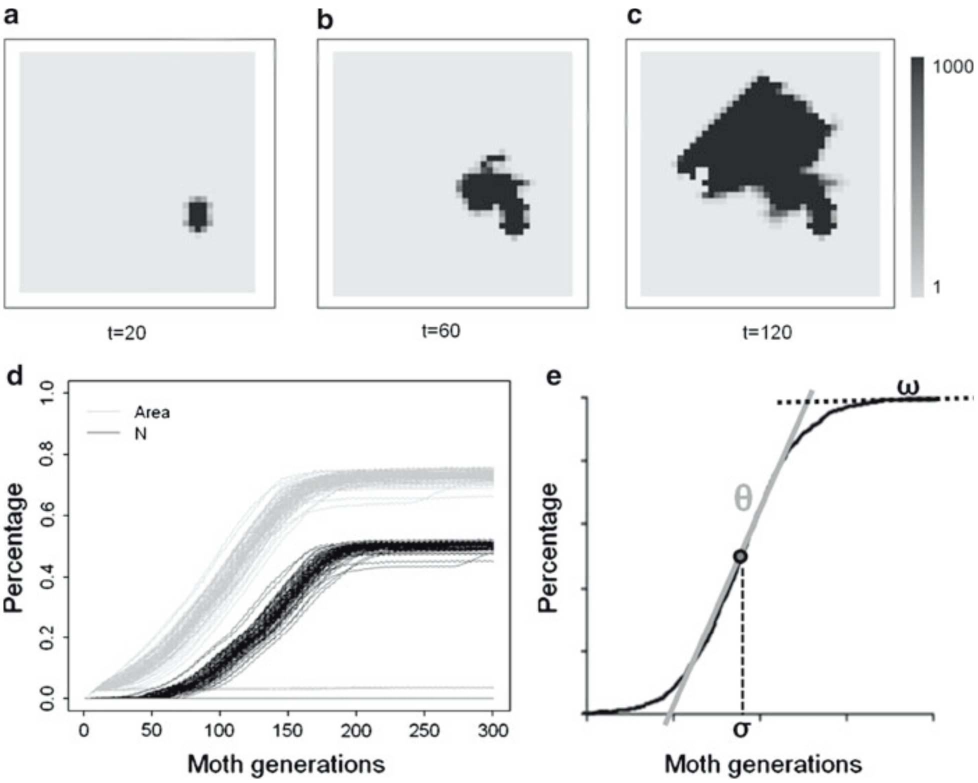


Fig. 2 Examples of model outputs: **a**–**c** spatial invasion represented by captions of CA grids at three different steps (*t*) of the invasion process; **d** temporal invasion throughout moth generations with the relative number of moths (*N*) and the proportion of invaded area (Area); **e** sigmoid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

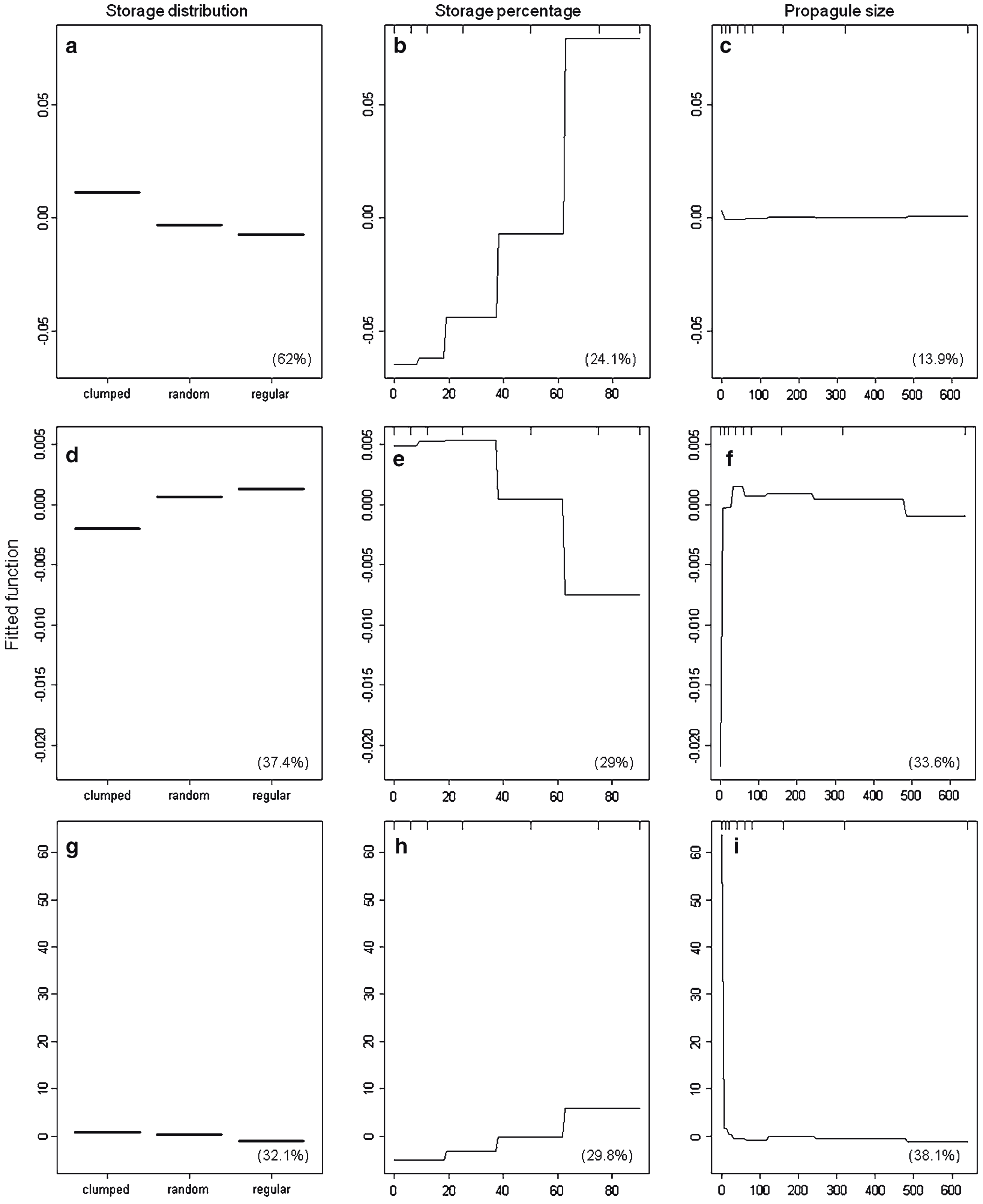


Fig. 3 Partial dependence plots for parameter ω (**a**–**c**), θ (**d**–**f**), and σ (**g**–**i**). Fitted functions have been centered by subtracting their mean. *Rug plots* at the inside top of plots show the distribution of data, in deciles, of the variable on the X-axis. *Values in parenthesis* indicate relative contribution of each factor to model output

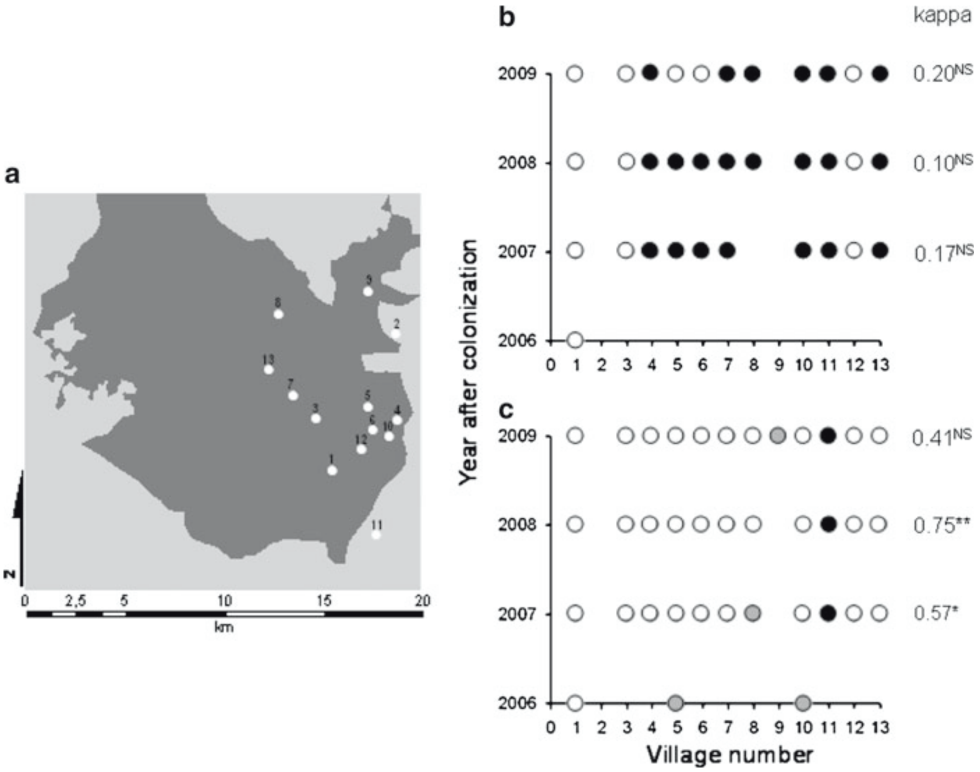


Fig. 4 Spatio-temporal validation of the model's outputs to field monitoring data from 2006 to 2009 in the Simiatug valley. **a** The 13 villages involved in the monitoring; **b** outputs of the basic model (no human influence); **c** outputs of the LDD scenario. *Black circles* represent cases where 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

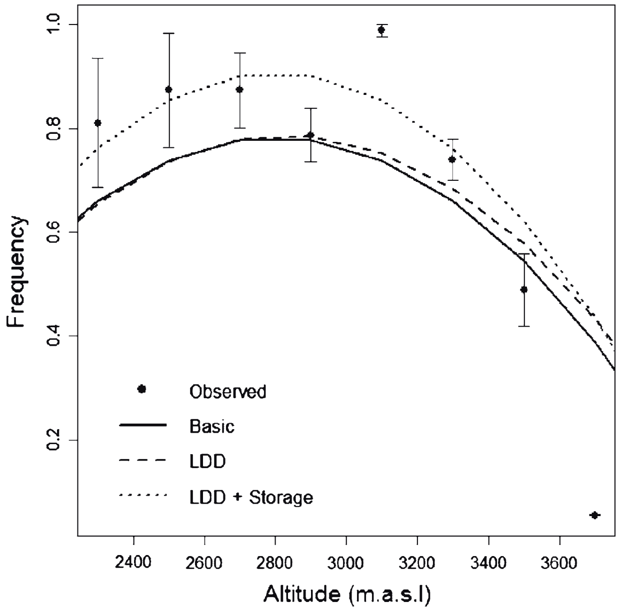


Fig. 5 Altitudinal validation of the model's outputs to field monitoring data in the Ecuadorian Andes. The figure shows the comparison between the observed altitudinal distribution in 85 sites of central Ecuador where moth abundance was sampled between 2006 and 2009 and predicted distribution by the 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 invasible 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.

Acknowledgments This work was part of the research conducted within the project *Innovative Approaches for integrated Pest Management in changing Andes* (C09-031) funded by the McKnight Foundation. We are grateful to Jérôme Casas and Isabelle Chuine for their helpful comments on previous versions of the manuscript. We also thank Carlos Carpio and Mario Hererra for their technical support during moth monitoring in the field, and Frederick Saltre for insightful discussions regarding models’ validation. We would also like to thank the editor, Kirk Maloney, and two anonymous reviewers whose constructive suggestions greatly improved the quality of our contribution. VCP was financed by grants from the French Embassy in Ecuador and from the *Département Soutien et Formation des communautés scientifiques du Sud* (DSF) of the IRD.

References

Anderson KL, Deveson TE, Sallam N, Congdon BC (2010) Wind-assisted migration potential of the island sugarcane planthopper *Eumetopina flavipes* (Hemiptera: Delphacidae): implications for managing incursions across an Australian quarantine frontline. J Appl Ecol 47:1310–1319

Baddeley A, Turner R (2005) Spatstat: an R package for analyzing spatial point patterns. J Stat Softw 12:1–42

Bonabeau E (2002) Agent-based modeling: methods and techniques for simulating human systems. Proc Natl Acad Sci USA 99:7280–7287

Bossenbroek JM, Kraft CE, Nekola JC (2001) Prediction of long-distance dispersal using gravity models: Zebra mussel invasion of inland lakes. Ecol Appl 11:1778–1788

Briggs CJ, Godfray HCJ (1996) The dynamics of insect-pathogen interactions in seasonal environments. Theor Popul Biol 50:149–177

Buchan LAJ, Padilla DK (1999) Estimating the probability of long-distance overland dispersal of invading aquatic species. Ecol Appl 9:254–265

Buston PM, Elith J (2011) Determinants of reproductive success in dominant pairs of clownfish: a boosted regression tree analysis. J Anim Ecol 80:528–538

Cacho OJ, Spring D, Hester S, Mac Nally R (2010) Allocating surveillance effort in the management of invasive species: a spatially-explicit model. Environ Model Softw 25:444–454

Cadotte M, McMahon S, Fukami T (2006) Conceptual ecology and invasion biology: reciprocal approaches to nature. Springer, Dordrecht

Cameron PJ, Walker GP, Penny GM, Wigley PJ (2002) Movement of potato tuberworm (Lepidoptera: Gelechiidae) within and between crops, and some comparisons with diamondback moth (Lepidoptera: Plutellidae). Environ Entomol 31:65–75

Cameron PJ, Wigley PJ, Elliott S, Madhusudhan VV, Wallace AR, Anderson JAD, Walker GP (2009) Dispersal of potato tuber moth estimated using field application of Bt for mark-capture techniques. Entomol Exp Appl 132:99–109

Carrasco LR, Mumford JD, MacLeod A, Harwood T, Grabenweger G, Leach AW, Knight JD, Baker RHA (2010) Unveiling human-assisted dispersal mechanisms in invasive alien insects: integration of spatial stochastic simulation and phenology models. Ecol Model 221:2068–2075

Dangles O, Carpio C, Barragan AR, Zeddam JL, Silvain JF (2008) Temperature as a key driver of ecological sorting among invasive pest species in the tropical Andes. Ecol Appl 18:1795–1809

Dangles O, Mesias V, Crespo-Perez V, Silvain JF (2009) Crop damage increases with pest species diversity: evidence from potato tuber moths in the tropical Andes. J Appl Ecol 46:1115–1121

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

Davies KF, Chesson P, Harrison S, Inouye BD, Melbourne BA, Rice KJ (2005) Spatial heterogeneity explains the scale dependence of the native–exotic diversity relationship. Ecology 86:1602–1610

Diggle PJ (2003) Statistical analysis of spatial point patterns, 2nd edn. Arnold/Hodder Headline Group, London

Elith J, Leathwick JR, Hastie T (2008) A working guide to boosted regression trees. J Anim Ecol 77:802–813

Ellenberg H (1979) Man's influence on tropical mountain ecosystems in South America—2nd Tansley Lecture. J Ecol 67:401–416

EPPO (2005) Data sheets on quarantined pests, *Tecia solanivora*. Bull OEPP/EPPO 35:399–401

Fenemore PG (1988) Host-plant location and selection by adult potato moth, *Phthorimaea operculella* (Lepidoptera, Gelechiidae)—a review. J Insect Phys 34:175–177

Fleiss JL (1971) Measuring nominal scale agreement among many raters. Psychol Bull 76:378–382

Foley DH (1985) Tethered flight of the potato moth, *Phthorimaea operculella*. Physiol Entomol 10:45–51

Gilbert M, Gregoire JC, Freise JF, Heitland W (2004) Long-distance dispersal and human population density allow the prediction of invasive patterns in the horse chestnut leafminer *Cameraria ohridella*. J Anim Ecol 73:459–468

Goslee SC, Peters DPC, Beck KG (2006) Spatial prediction of invasion success across heterogeneous landscapes using an individual-based model. Biol Invasions 8:193–200

Hanafi A (1999) Integrated pest management of potato tuber moth in field and storage. Potato Res 42:373–380

Hanski I, Gaggiotti OE (2004) Ecology, genetics, and evolutions of metapopulations. Elsevier, Amsterdam

Hanski I, Alho J, Moilanen A (2000) Estimating the parameters of survival and migration of individuals in metapopulations. Ecology 81:239–251

Harris CM, Park KJ, Atkinson R, Edwards C, Travis JMJ (2009) Invasive species control: incorporating demographic data and seed dispersal into a management model for *Rhododendron ponticum*. Ecol Inform 4:226–233

Hastings A, Cuddington K, Davies KF, Dugaw CJ, Elmendorf S, Freestone A, Harrison S, Holland M, Lambrinos J, Malvadkar U, Melbourne BA, Moore K, Taylor C, Thomson D (2005) The spatial spread of invasions: new developments in theory and evidence. Ecol Lett 8:91–101

Herben T, Munzbergova Z, Milden M, Ehrlen J, Cousins SAO, Eriksson O (2006) Long-term spatial dynamics of *Succisa pratensis* in a changing rural landscape: linking dynamical modelling with historical maps. J Ecol 94:131–143

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25:1965–1978

Hufkens K, Ceulemans R, Scheunders P (2008) Estimating the ecotone width in patchy ecotones using a sigmoid wave approach. Ecol Inform 3:97–104

Hutchings MJ, John EA, Stewart AJA (eds) (2000) The ecological consequences of environmental heterogeneity. Blackwell, Oxford

Jongejans E, Skarpaas O, Shea K (2008) Dispersal, demography and spatial population models for conservation and control management. Perspect Plant Ecol Evol Syst 9: 153–170

Keasar T, Kalish A, Becher O, Steinberg S (2005) Spatial and temporal dynamics of potato tuberworm (Lepidoptera: Gelechiidae) infestation in field-stored potatoes. J Econ Entomol 98:222–228

Keller S (2003) Integrated pest management of the potato tuber moth in cropping systems of different agroecological zones. Margraf Publishers, Germany

Körner C (2007) The use of 'altitude' in ecological research. Trends Ecol Evol 22:569–574

Lewis MA, Pacala S (2000) Modeling and analysis of stochastic invasion processes. J Math Biol 41:387–429

Liebhold AM, Tobin PC (2008) Population ecology of insect invasions and their management. Annu Rev Entomol 53:387–408

MA (2003) Ecosystems and human well-being: a framework for assessment. Island Press, Washington

MAE, EcoCiencia (2005) Proyecto Indicadores de Biodiversidad para Uso Nacional y el Programa de Biodiversidad, Páramos y otros Ecosistemas Frágiles. Project Coordinators: Ángel Onofa (MAE) and Malki Sáenz (EcoCiencia): Quito, Ecuador

Manel S, Williams HC, Ormerod S (2001) Evaluating presence–absence models in ecology: the need to account for prevalence. J Appl Ecol 38:921–931

Melbourne BA, Cornell HV, Davies KF, Dugaw CJ, Elmendorf S, Freestone AL, Hall RJ, Harrison S, Hastings A, Holland M, Holyoak M, Lambrinos J, Moore K, Yokomizo H (2007) Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? Ecol Lett 10:77–94

Miller TEX (2007) Demographic models reveal the shape of density dependence for a specialist insect herbivore on variable host plants. J Anim Ecol 76:722–729

Miller TEX, Tenhumberg B (2010) Contributions of demography and dispersal parameters to the spatial spread of a stage-structured insect invasion. Ecol Appl 20:620–633

Moilanen A (1999) Patch occupancy models of metapopulation dynamics: efficient parameter estimation using implicit statistical inference. Ecology 80:1031–1043

Moilanen A (2004) SPOMSIM: software for stochastic patch occupancy models of metapopulation dynamics. Ecol Model 179:533–550

Muirhead JR, Leung B, van Overdijk C, Kelly DW, Nandakumar K, Marchant KR, MacIsaac HJ (2006) Modelling local and long-distance dispersal of invasive emerald ash borer *Agrilus planipennis* (Coleoptera) in North America. Divers Distrib 12:71–79

Munkemuller T, Travis JMJ, Burton OJ, Schiffers K, Johst K (2011) Density-regulated population dynamics and conditional dispersal alter the fate of mutations occurring at the front of an expanding population. Heredity 106:678–689

Nehrbass N, Winkler E (2007) Is the Giant Hogweed still a threat? An individual-based modelling approach for local invasion dynamics of *Heracleum mantegazzianum*. Ecol Model 201:377–384

Nehrbass N, Winkler E, Mullerova J, Pergl J, Pysek P, Perglova I (2007) A simulation model of plant invasion: long-distance dispersal determines the pattern of spread. Biol Invasions 9:383–395

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

Pauchard A, Kueffer C, Dietz H, Daehler CC, Alexander J, Edwards PJ, Arevalo JR, Cavieres LA, Guisan A, Haider S, Jakobs G, McDougall K, Millar CI, Naylor BJ, Parks CG, Rew LJ, Seipel T (2009) Ain't no mountain high enough: plant invasions reaching new elevations. Front Ecol Environ 7:479–486

Perry GLW (2004) SpPack: spatial point pattern analysis in Excel using Visual Basic for Applications (VBA). Environ Model Softw 19:559–569

Pitt JPW, Worner SP, Suarez AV (2009) Predicting Argentine ant spread over the heterogeneous landscape using a spatially explicit stochastic model. Ecol Appl 19:1176–1186

Prasad A, Iverson L, Peters M, Bossenbroek J, Matthews S, Davis Sydnor T, Schwartz M (2010) Modeling the invasive emerald ash borer risk of spread using a spatially explicit cellular model. Landscape Ecol 25:353–369

Puillandre N, Dupas S, Dangles O, Zeddam JL, Capdevielle-Dulac C, Barbin K, Torres-Leguizamon M, Silvain JF (2008) Genetic bottleneck in invasive species: the potato tuber moth adds to the list. Biol Invasions 10:319–333

R Development Core Team (2009) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0,http://www.R-project.org

R Development Core Team (2010) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, http://www.R-project.org

Rebaudo F, Crespo-Pérez V, Dangles O (2010) SimPolilla© A cellular automaton to describe a pest invasion within the northern Andes. CIRAD, http://cormasciradfr/en/applica/SimPolillahtm. Accessed 4 Aug 2010

Rebaudo F, Crespo-Pérez V, Silvain J-F, Dangles O (2011) Agent-based modeling of human-induced spread of invasive species in agricultural landscapes: insights from the potato moth in Ecuador. JASS 14:7

Régnière J, Turgeon JJ (1989) Temperature-dependent development of *Zeiraphera canadensis* and simulation of its phenology. Entomol Exp Appl 50:185–193

Régnière J, Nealis V, Porter K (2009) Climate suitability and management of the gypsy moth invasion into Canada. Biol Invasions 11:135–148

Richardson DM, Pysek P (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. Prog Phys Geogr 30:409–431

Ridgeway G (2010) Package 'gbm' version 1.6-3.1. http://cranr-projectorg/web/packages/gbm/gbmpdf. Accessed 2 May 2011

Rothschild GHL (ed) (1986) The potato moth—an adaptable pest of short-term cropping systems. Wiley, Canberra

Roux O, Baumgartner J (1998) Evaluation of mortality factors and risk analysis for the design of an integrated pest management system. Ecol Model 109:61–75

Schreiber SJ, Lloyd-Smith JO (2009) Invasion dynamics in spatially heterogeneous environments. Am Nat 174:490–505

Sebert-Cuvillier E, Simon-Goyheneche V, Paccaut F, Chabrerie O, Goubet O, Decocq G (2008) Spatial spread of an alien tree species in a heterogeneous forest landscape: a spatially realistic simulation model. Landscape Ecol 23:787–801

Shea K, Jongejans E, Skarpaas O, Kelly D, Sheppard AW (2010) Optimal management strategies to control local population growth or population spread may not be the same. Ecol Appl 20:1148–1161

Soons MB, Messelink JH, Jongejans E, Heil GW (2005) Habitat fragmentation reduces grassland connectivity for both short-distance and long-distance wind-dispersed forbs. J Ecol 93:1214–1225

Suarez AV, Holway DA, Case TJ (2001) Patterns of spread in biological invasions dominated by long-distance jump dispersal: insights from Argentine ants. Proc Natl Acad Sci USA 98:1095–1100

Travis JMJ, Smith HS, Ranwala SMW (2010) Towards a mechanistic understanding of dispersal evolution in plants: conservation implications. Divers Distrib 16:690–702

Travis JMJ, Harris CM, Park KJ, Bullock JM (2011) Improving prediction and management of range expansions by combining analytical and individual-based modelling approaches. Methods Ecol Evol. doi:10.1111/j.2041-210X.2011.00104.x. Published Online

Wu H, Malafant KWJ, Pendridge LK, Sharpe PJH, Walker J (1987) Simulation of two-dimensional point patterns. Application of a lattice framework approach. Ecol Model 38:299–308

Yathom S (1968) Phenology of the tuber moth *Gnorimoschema operculella* Zell. in Israel in spring. Isr J Agric Res 18:89–90

APPENDICES CHAPTER 1

APPENDIX S1.- Description of the cellular automata basic scenario

This appendix describes our cellular automaton's basic scenario (no human influence) in detail. Description is inspired by the ODD protocol (Overview, Design concepts, and Details) for describing agent-based and cellular automata models (Grimm et al. 2006, Appendix A). It first consists on an overview of model structure and then describes each sub-model in detail.

Model overview

Our model simulates the spatio-temporal dynamics of potato tuber moth invasion. We built our model using the Cormas modeling platform (CIRAD, France, http://cormas.cirad.fr) based on the VisualWorks programming environment.

State variables and scales

The basic module is based on biological and ecological rules derived from field and laboratory experimental data for *T. solanivora*. State variables are divided into those related to the physical and climatic environment (geographic variables) and those related to moth abundance.

Geographical variables.- Each cell i of our model grid is characterized by a mean elevation E_i (in m.a.s.l.), the temperature $T_{i:m}$ of month m (in °C), the precipitation $L_{i:m}$ of month m (in mm) and the habitat quality $Q_{i,}$ defined by the presence (Q_i=1) or absence (Q_i=0) of cultivated potato fields in the cell. All these variables are summarized in Table 1 and Fig 1. The first three variables were obtained from the WorldClim data set (Hijmans et al. 2005). The latter was obtained from the BINU Project (Biodiversity Indicators for National Use, MAE and EcoCiencia 2005). Both temperature and precipitation data corresponded to the means of the period 1961-1990 (Hijmans et al. 2005).

Moth abundance variables.- Moth life cycle can be differentiated into four life stages: egg, larva, pupa, and adult. *T. solanivora*'s larval stage can be further divided into four instars. However, for the purposes of this study, all larval instars were combined into a single life stage because it was not possible to adequately segregate the development and survival functions for each instar inside the potato tuber (see Dangles et al. 2008). Furthermore, since moth immature stages constitute a biological and ecological unit (sharing similar life environments), it is likely that segregating development and survival functions for each larval instar would not have given more accuracy to the model.

We had three outcome variables in each cell of the model: 1) the abundance of immatures J_i, which grouped eggs, larvae and pupae, 2) the abundance of adults M_i, and 3) the abundance of gravid females G_i (Table 1, Fig. 1). These three variables represented the higher-level variables of the model, i.e. the variables that contained information deduced from the state variables (*sensu* Grimm et al. 2006).

Table 1. State and higher-level variables of the basic module.

Variable name	Description	Parameter	Units
State variables			
Elevation	Elevation on the study zone per cell *i*	E_i	m
Temperature	Average temperature per cell *i* and month *j*	$T_{i,m}$	ºC
Precipitation	Average precipitation per cell *i* and month *j*	$L_{i,m}$	mm
Habitat quality	Presence of potato cultures in cell *i*	Q_i	Boolean
Higher-level variables			
	Immature abundance in cell *i*	J_i	Number of individuals
Moth abundance	Adult abundance in cell *i*	M_i	Number of individuals
	Gravid female abundance in cell *i*	G_i	Number of individuals

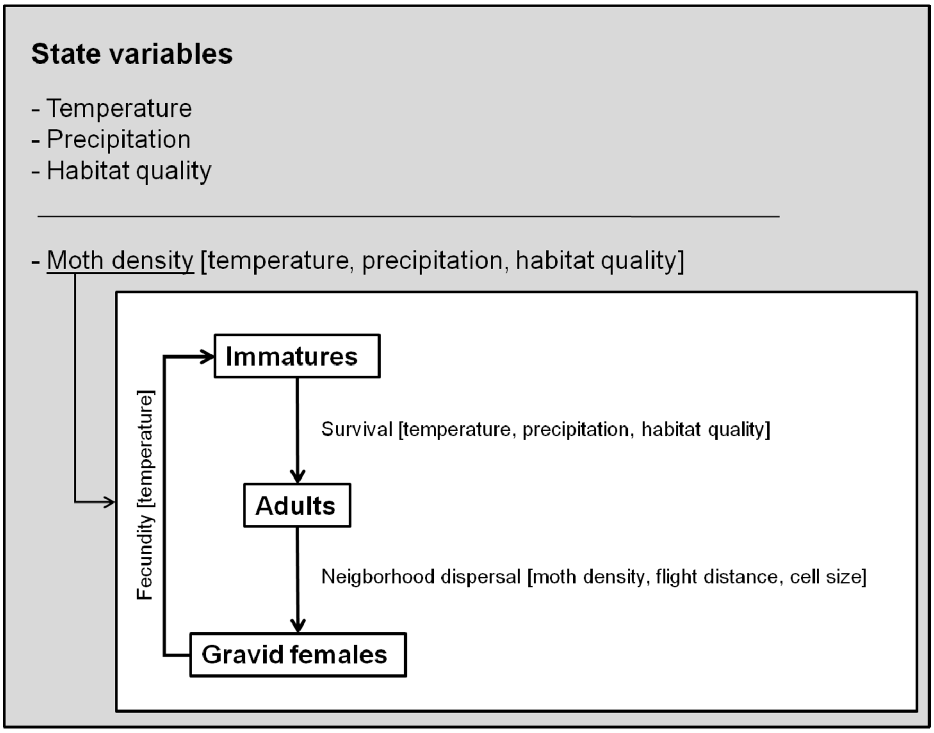


Fig.1. Schematic model structure. Variables in the grey area are the state variables of the model. The white zone represents higher-level variables that contain information deduced from state variables.

Scales

Each time step represents one moth generation (normalized to 3 months at 15 °C). We chose a 500 × 500 m scale for cells (i.e. 0.25 km^2) to fit the level of precision available on the land use data. Elevation, temperature, and precipitation had a 1 km^2 resolution, so that inside a square of 4 cells, these parameters had the same value.

Sub models

In this section we first describe model initialization and variable setting and then detail each sub model used to update the cells at each generation.

Initialization

At the beginning of each simulation, we placed an inoculum of 90 individuals in the Simiatug village, the main source of moth infestation in the region (Dangles et al. 2010). This inoculum size represents the median value for *T. solanivora* pupae abundance in infested potato sacks (Padilla and Dangles, unp. data, $n = 21$ sacks, SD = 23). We therefore simulated what likely happened after road rehabilitation in 2006 using one potato sack as the inoculum. We set the adult moth carrying capacity of each cell to 1000 individuals (see main text). After the initial inoculum, moth spread was observed and recorded throughout successive generations.

State variables setting

Temperature and precipitation.- As the model's time step was fixed to one *T. solanivora* generation, we used temperature and precipitation data corresponding to the mean of three consecutive months.

Habitat quality.- Data of the land use layer allowed us to identify potential zones with potato cultures (termed "short cycle crops") where moth can realize their life cycle. Complementary field observations were made to check the accuracy of the data, especially in the rapidly expanding agricultural frontier to higher altitudes. Cells with short cycle crops were given the value of 1 and allowed moth survival whereas the rest were given a value of 0 and hampered survival.

Sub models – Spatial dynamics of moth populations

Because survival rates and reproduction of moths depend on their physiological stage (eggs, larvae, pupae, adults), we used a stage-structured model (Briggs and Godfray 1995, 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 (adults) and reproduction (gravid females) (Fig.1). Climate dependent survival was a function of both temperature and precipitation. Adult dispersal, through diffusion, was influenced by moth density, flight distance, and cell size. Reproduction depended solely on temperature as it has been shown for other Gelechiid species (e.g. *Phthorimaea operculella*) that precipitation has little direct influence on this parameter (Roux 1993). Information about the effect of temperature on survival and reproduction and of precipitation on survival was obtained from laboratory experiments and field data, respectively.

Immature moth survival

Demographically based mortality.- Following Roux (1993), we considered that the overall forces of mortality among immature instars were the sum of demographically based and climate related forces. We included two sources of demographically based mortality: dispersal related mortality λ_{disp} occurring between each immature stage (for example when a newly hatched larva searches for a tuber) and predation λ_{pred} (Roux 1993, Roux and Baumgartner 1998). The survival function $S_{disp,pred}$ for each cohort was expressed as follows:

$$S_{disp,pred}(t) = e^{-(\lambda_{disp}+\lambda_{pred})t} \tag{1}$$

where t denotes days after cohort initiation.

The lack of biological data on *T. solanivora*'s mortality compelled us to fix the λ_{disp} and λ_{pred} parameter to 0.060 and 0.145 respectively, based on data from Roux (1993, Table 4.8) for the Gelechiid moth *P. operculella*. Based on Fig. 4.18 and Table 4.8 in Roux (1993), presenting $S_{disp,pred}$ as a function of time, we chose t =2 days as this is the approximate amount of time it takes newly hatched larvae to get to the tubers (Dangles and Mesias unpbl. data). We are not aware of data on demographically based mortality of larvae living inside the tubers.

Temperature dependent survival.- Data on survival for immature stages as a function of temperature were acquired from two sources. First, we compiled published data from laboratory experiments performed using moth populations from different regions in the Northern Andes (Notz 1995, Castillo 2005, Dangles et al. 2008). Second, we used unpublished data obtained within the last 8 years in the Entomology Laboratory of the Pontificia Universidad Católica del Ecuador (PUCE, Pollet, Barragan and Padilla, unpublished data). For these two sources, only data acquired under constant temperatures (± 2 °C) were considered. In all studies, relative humidity ranged from 70 to 90 %, values above any physiological stress for these moths (Roux 1993). These survival data as a function of temperature, *S(T)*, are presented in Fig. 2.

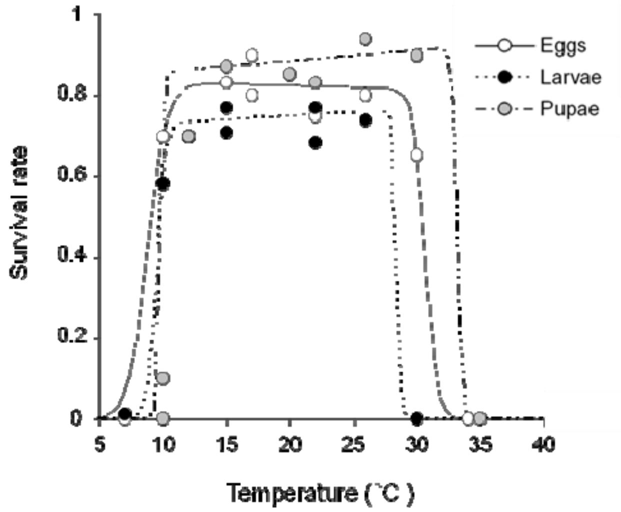


Fig. 2. Effect of constant temperatures on the survival rate *S(T)* of *T. solanivora*'s immature life stages as fitted by eq. 2. Circles represent observed survival rates and lines correspond to the adjusted model.

Several models have been used to describe the relationship between temperature and process rates in insects, like the Sharpe and DeMichele model (Sharpe and DeMichele 1977), the Extended von Foerster model (Gilbert et al. 2004) and the distributed delay model (Dangles et al. 2008). We modeled temperature-related survival rates of immature moth using the Sharpe and DeMichele equation that has already been successfully used to simulate tuber moth development and survival (see Roux 1993):

$$S(T) = \frac{a\frac{T}{298.16}\exp[b(\frac{1}{298.16}-\frac{1}{T})]}{1+\exp[\frac{c}{R}(\frac{1}{d}-\frac{1}{T})]+\exp[\frac{e}{R}(\frac{1}{f}-\frac{1}{T})]} \qquad (2)$$

with T the fixed mean temperature expressed in °K, R the universal gas constant (1.987 cal.°K^{-1}.mol^{-1}), and a, b, c, d, e, and f parameters to be estimated. Model adjustment was performed using least square minimization techniques in the Library (Mass) of R (R Development Core Team 2009). Results are shown in Fig. 2 and. Table 2.

Table 2. Parameter values of the kinetic model (eq. 2) describing the stage specific survival rate $S(T)$ of *T. solanivora* at constant temperatures. Note that temperature is given in degrees Kelvin in the model (parameters d and f).

Stage	a	b	c	d	e	f	R^2
Egg	0.822	-758.5	-212100	281.9	405200	303.8	0.919
Larva	0.758	-180.2	-475700	282.7	1298000	301.5	0.902
Pupa	0.900	-73.72	-1263000	286.5	1095000	306.3	0.892

Adjustment of moth generation length at different temperatures.- The time step of our model was one moth generation, fixed at three months. In order to account for differences in generation length among individuals growing at different temperatures (for example along the altitudinal gradient), we made an adjustment on immature abundance (J_i) as a function of cell temperature. This adjustment affected only a small proportion of individuals since most of them had a generation period close to three months in the studied region (Dangles et al. 2008).

For this adjustment we first compiled published (Notz 1995, Castillo 2005, Dangles et al. 2008) and unpublished data (Pollet, Barragan and Padilla, unpublished data) on *T. solanivora* development rates at various constant temperatures. We adjusted these data to the Sharpe and DeMichel model with the same procedure as for the survival data. Results are shown in Fig. 3 and Table 3 (note that to differentiate from survival rate parameters, parameters for developmental rate are followed by a D in subscript).

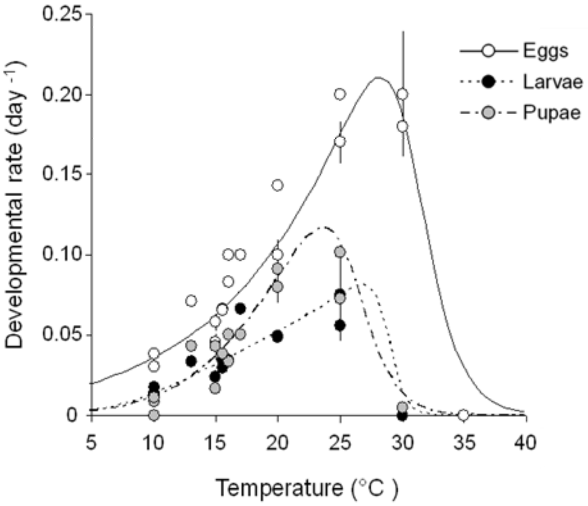


Fig. 3. Effect of constant temperatures on the stage specific developmental rate *D(T)* of *T. solanivora*'s immature life stages. Circles represent observed survival rates and lines correspond to the adjustment of the Sharpe and DeMichel equation (eq. 2).

Table 3. Parameter values of the kinetic model (eq. 2) describing the stage specific developmental rate response of *T. solanivora* to constant temperatures. Note that temperature is given in degrees Kelvin in the model.

Stage	a_D	b_D	c_D	d_D	e_D	f_D	R^2
Egg	0.179	17250	-48000	265.2	121830	304.2	0.887
Larva	0.076	11000	-50000	283.1	275000	302.1	0.876
Pupa	0.187	11500	-35000	290.0	125000	299.5	0.898

Developmental rates for immature moths in each cell *i* of the model were then calculated and divided by that at 15 °C (temperature at which developmental time corresponds to 3 months). The result of this division was then multiplied by the number of immature moths (J_i) in the corresponding cell.

Precipitation dependent mortality.- We were not aware of any mechanistic model describing the effect of precipitation on moth survival so we decided to incorporate precipitation in our model using empirical field data. Heavy rainfall events such as the El

Niño event in late 1997 (Barragán et al. 2004) and in late 2007 to July 2008 (Dangles and Carpio, unpubl. data) significantly affected moth population abundance in the field. Other studies also registered a decrease in the number of *T. solanivora* adults collected during rainy periods (Barreto et al. 2004, Niño 2004) and this coincides with results found for *P. opercullela* (Rothschild 1986) and other moth species like the Gypsy moth (*Lymantria dispar*, Pernek et al. 2008). Therefore, we included an effect of rainfall over a fixed precipitation threshold which was chosen based on climatic data and corresponding field abundance data (Dangles et al. 2008, Appendix A http://www.esapubs.org/archive/appl/A018/062/appendix-A.htm). Moth abundance was reduced by 80 %, when the cumulated rainfall during 3 consecutive months was higher than 600 mm (i.e. about 2.4 times more rainfall than on normal years).

Adult moth survival

We considered that adult mortality before reproduction was negligible since, according to the literature, mating in most Lepidoptera, including Gelechiidae, often occurs within 24 h of emergence (Webster and Carde 1982, Cameron et al. 2005).

Adult neighborhood dispersal:

T. solanivora's dispersal takes place when adults fly in order to find mates and/or suitable oviposition sites in potato fields or in potato storage structures (Barragán 2005). To include neighborhood dispersal into our model we considered two factors: 1) the density dependent nature of emigration rate (Eizaguirre et al. 2004; BenDor and Metcalf 2006), and 2) the decrease in emigration rate with increasing distances (Cameron et al. 2002). These factors were integrated into our cellular automata through four steps:

1) Fraction of adults emigrating from cell *i* (V_{Mi}) as a function of adult density.– Based on BenDor and Metcalf (2006) we assumed that the fraction of adults emigrating per generation (V_{Mi}), with respect to population density, followed an S-shaped curve, which levels out as density approaches 50 % of the carrying capacity, *K* (Fig. 4).

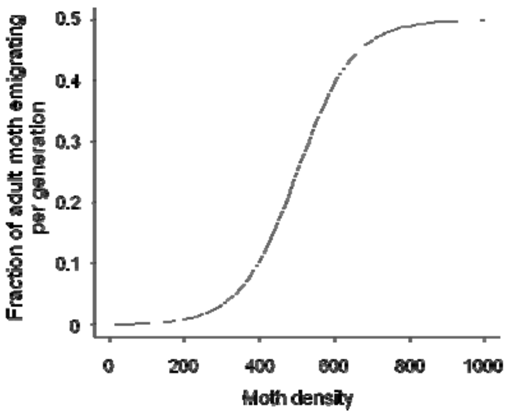


Fig. 4. Fraction of *T. solanivora* adults emigrating as a function of adult density (eq.5). Carrying capacity (K) was fixed to 1000 adults per cell.

We calculated V_{Mi} using eq. 3 as follows:

$$V_{Mi} = \frac{0.5}{1 + \exp\left[-\frac{M_i - \beta}{\psi} \right]} \tag{3}$$

where M_i is the number of adults in cell i, β is the rate of increase in migration with density (transition center) and ψ is the transition width. Due to the absence of data for potato moth about the parameters of the S-shaped curve, we fixed arbitrarily $\beta = 500$ and $\psi = 75$, i.e. we assumed a symmetric pattern of the curve from a moth density of 0 to half of *K*. A previous sensitivity analysis revealed that these two parameters had little influence on the overall dispersion of moths (Rebaudo and Dangles 2008).

2) Emigration rate (P_{dist}) as a function of distance.– Following Cameron et al. (2002) for *P. operculella*, we calculated the probability of moths flying a given distance (δ) with eq. 4:

$$P_{dist} = e^{-\varepsilon * \delta} \tag{4}$$

where ε is a fixed parameter of emigration rate (see below). As stated in the main text, lack of data regarding *T. solanivora*'s flight capacity forced us to fix maximum dispersal distance to

250 m, the value measured for *P. operculella*. Following Cameron et al. (2002), we used a maximum value of ε of 0.015.

3) Including neighborhood dispersal in our model.– Given the discrete nature of cellular automata, in both time and space, we could not include dispersal as a continuous variable. Therefore, for each time step of the simulation, we calculated the probability of adult moths crossing the border of their current cell (P_{cross}). First, we assumed that moths moved inside the cell either horizontally or vertically and that they flew to the closest of the four neighboring cells. Then we considered that the probability of them crossing the cell depended on the distance flown and on cell's dimensions as follows:

$$P_{cross}(A,C,\delta) = \begin{cases} 1 & \delta > 250 \\ \dfrac{(A-(C-2*\delta)^2}{A} & 0 < \delta \leq 250 \end{cases} \tag{5}$$

where A represents the cell's surface and C its length. P_{cross} was then multiplied by the probability of moths emigrating (eq. 6) in order to obtain the actual probability of moths leaving a cell, which we named $P_{leaving}$:

$$P_{leaving} = P_{cross} * P_{dist} \tag{6}$$

4) Number of moths dispersing to adjacent cells (N_{disp}).– Finally, the number of moths dispersing to neighboring cells was calculated as follows:

$$N_{disp} = V_{Mi} * P_{leaving} \tag{7}$$

Fig. 5 shows effective dispersal rate in relation to moth density and flight distance.

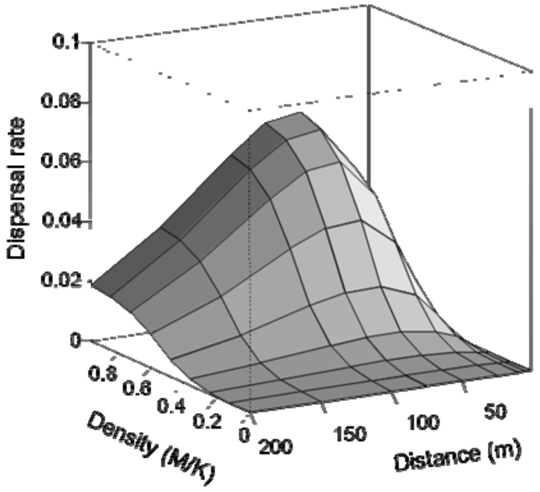


Fig.5. Effective dispersal rate considering moth density and flight distance.

Moth reproduction

Insect reproduction is influenced by various factors including mating rate, sex ratio and female fecundity, which we all detail below for potato moth.

Mating rate.– For *P. operculella* this process was found to be correlated with age, sex ratio and weight of individuals, but also with distance between individuals (Makee and Saour 2001, Cameron et al. 2005). Most Lepidoptera females tend to mate within 24 h of emergence (Webster and Carde 1982, Makee and Saour 2001). According to the latter, with a sex ratio of 1:1, mating rate is approximately 0.9 after that same period of time. To our knowledge, no specific studies have been conducted on *T. solanivora*'s mating rate in natural conditions, and laboratory measurements may frequently represent an overestimation since laboratory females have little opportunity to avoid mating (Reinhardt et al. 2007). Therefore, in the absence of data we assumed a mating rate of 0.9.

Sex ratio.– Studies have documented a sex ratio of roughly 1:1 for *T. solanivora* (Herrera 1998) and *P. operculella* (Makee and Saour 2003). Unpublished data from colonies of *T. solanivora* reared at the PUCE confirmed these results (Mesías and Dangles, unpubl. data).

Female fecundity.– As for survival and development rates, data on female fecundity as a function of constant temperature were acquired from published (Notz 1995, Castillo 2005, Dangles et al. 2008) and unpublished data (Pollet, Barragan and Padilla, unpublished data). We adjusted these to a gamma function (eq. 8), already used to model Gelechiid fecundity as a function of temperature (Sporleder et al. 2004), to obtain the temperature-dependent fecundity curve:

$$F(T) = o + p * \exp\left(-\frac{T-q}{r}\right)\left(\frac{\frac{T-q}{r}+s-1}{s-1}\right)^{s-1} \qquad (8)$$

with T the mean fixed temperature in this case in °C and o, p, q, r and s parameters to be estimated. Parameter estimation was performed using least square minimization techniques in the Library (Mass) of R (R Development Core Team, 2009). *F(T)* is presented in Fig. 7, with the following estimation of curve parameters: o = -21.62, p = 345.50, q = 18.66, and r = 0.32, and s = 243.00 (R^2 = 0.865).

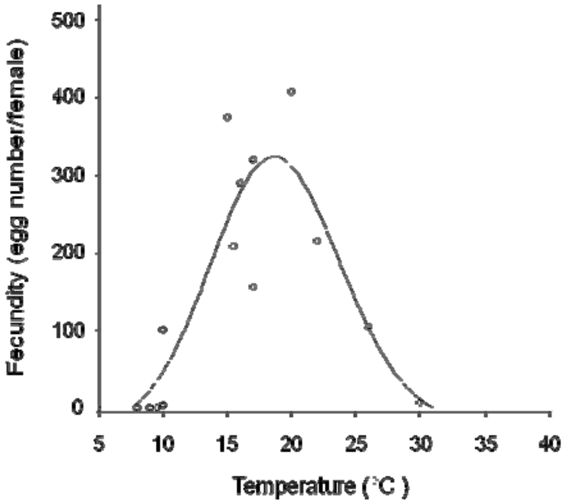


Fig.6. Effect of constant temperatures on moth fecundity *F(T)* as fitted by equation 8.

REFERENCES

Barragán, A. 2005. Identificación, biología y comportamiento de las polillas de la papa en el Ecuador. Boletín PROMSA, MAG-PUCE, Quito, Ecuador.

Barragán, A., A. Pollet, J. M. Prado, A. Lagnaoui, G. Onore, I. Aveiga, X. Lery, and J. L. Zeddam, editors. 2004. La polilla guatemalteca *Tecia solanivora* (Povolny) (Lepidoptera:Gelechiidae) en Ecuador. Diagnóstico y perspectivas de manejo bajo un método de predicción. Centro de Biodiversidad y Ambiente, Escuela de Biología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador.

Barreto, N., Espitia, E., R. Galindo, E. Gordo, L. Cely, G. Sánchez, and A. López-Ávila, editors. 2004. Fluctuación de la población de *Tecia solanivora* (Povolny) (Lepidoptera : Gelechiidae) en tres intervalos de altitud en Cundinamarca y Boyacá, Colombia. Centro de Biodiversidad y Ambiente, Escuela de Biología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador.

BenDor, T. K., and S. S. Metcalf. 2006. The spatial dynamics of invasive species spread. System Dynamics Review **22**:27-50.

Briggs, C. J., and H. C. J. Godfray. 1995. The Dynamics of Insect-Pathogen Interactions in Stage-Structured Populations. American Naturalist **145**:855-887.

Cameron, P. J., G. P. Walker, G. M. Penny, and P. J. Wigley. 2002. Movement of potato tuberworm (Lepidoptera: Gelechiidae) within and between crops, and some comparisons with diamondback moth (Lepidoptera: Plutellidae). Environmental Entomology **31**: 65-75.

Cameron, P. J., A. R. Wallace, V. V. Madhusudhan, P. J. Wigley, M. S. Qureshi, and G. P. Walker. 2005. Mating frequency in dispersing potato tuber moth, *Phthorimaea operculella*, and its influence on the design of refugia to manage resistance in Bt transgenic crops. Entomologia Experimentalis Et Applicata **115**:323-332.

Castillo, G. M. 2005. Determinación del ciclo de vida de las polillas de la papa *Symmetrischema tangolias* (Gyen) y *Tecia solanivora* (Povolny) bajo condiciones controladas de laboratorio. Universidad Central del Ecuador, Quito.

Dangles, O., C. Carpio, A. R. Barragan, J. L. Zeddam, and J. F. Silvain. 2008. Temperature as a key driver of ecological sorting among invasive pest species in the tropical Andes. Ecol Appl **18**:1795-1809.

Dangles, O., C. Carpio, M. Villares, F. Yumisaca, B. Liger, F. Rebaudo, and J. F. Silvain. 2010. Community-Based Participatory Research Helps Farmers and Scientists to Manage Invasive Pests in the Ecuadorian Andes. AMBIO. **39**:325-335.

Eizaguirre, M., C. Lopez, and R. Albajes. 2004. Dispersal capacity in the Mediterranean corn borer, *Sesamia nonagrioides*. Entomologia Experimentalis Et Applicata **113**:25-34.

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

Grimm, V., U. Berger, F. Bastiansen, S. Eliassen, V. Ginot, J. Giske, J. Goss-Custard, T. Grand, S. K. Heinz, G. Huse, A. Huth, J. U. Jepsen, C. Jorgensen, W. M. Mooij, B. Muller, G. Pe'er, C. Piou, S. F. Railsback, A. M. Robbins, M. M. Robbins, E. Rossmanith, N. Ruger, E. Strand, S. Souissi, R. A. Stillman, R. Vabo, U. Visser, and D. L. DeAngelis. 2006. A standard protocol for describing individual-based and agent-based models. Ecological Modelling **198**:115-126.

Herrera, F. 1998. La polilla guatemalteca de la papa: biología, comportamiento y prácticas de manejo integrado. Corporación Colombiana de Investigación Agropecuaria (CORPOICA), Bogotá, Colombia.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. Int J Climatol **25**:1965-1978.

MAE, and EcoCiencia. 2005. Proyecto Indicadores de Biodiversidad para Uso Nacional y el Programa de Biodiversidad, Páramos y otros Ecosistemas Frágiles. Project Coordinators: Ángel Onofa (MAE) and Malki Sáenz (EcoCiencia).Quito, Ecuador.

Makee, H., and G. Saour. 2001. Factors influencing mating success, mating frequency, and fecundity in *Phthorimaea operculella* (Lepidoptera: Gelechiidae). Environmental Entomology **30**:31-36.

Makee, H., and G. Saour. 2003. Noninherited sterility in irradiated Phthorimaea operculella females. Journal of Applied Entomology **127**:489-493.

Miller, T. E. X. 2007. Demographic models reveal the shape of density dependence for a specialist insect herbivore on variable host plants. Journal of Animal Ecology **76**:722-729.

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

Notz, A. 1995. Influencia de la temperatura sobre la biologia de *Tecia solanivora* (Povolny) (Lepidoptera: Gelechiidae) criadas en tuberculos de papa *Solanum tuberosum* L. Boletín de Entomología Venezolana **11**:49-54.

Pernek, M., I. Pilas, B. Vrbek, M. Benko, B. Hrasovec, and J. Milkovic. 2008. Forecasting the impact of the Gypsy moth on lowland hardwood forests by analyzing the cyclical pattern of population and climate data series. Forest Ecology and Management **255**:1740-1748.

R. 2009. R: A language and environment for statistical computing. Page Development Core Team R Foundation for Statistical Computing, Vienna, Austria.

Rebaudo, F., and O. Dangles. 2008. Developing multi-agent based models to strengthen food security in the Northern Andes: Application to invasive agricultural pests in Central Ecuador. Technical Assistance Report for the McKnight Foundation, Quito, Ecuador.

Reinhardt, K., G. Kohler, S. Webb, and D. Childs. 2007. Field mating rate of female meadow grasshoppers, *Chorthippus parallelus*, estimated from sperm counts. Ecological Entomology **32**:637-642.

Rothschild, G. H. L., editor. 1986. The potato moth – an adaptable pest of short-term cropping systems. John Wiley & Sons, Canberra, Australia.

Roux, O. 1993. Population ecology of potato tuber moth *Phthorimaea operculella* (Zeller) (Lepidoptera:Gelechiidae) and design of an integrated pest management program in Tunisia. SWISS FEDERAL INSTITUTE OF TECHNOLOGY, Zurich.

Roux, O., and J. Baumgartner. 1998. Evaluation of mortality factors and risk analysis for the design of an integrated pest management system. Ecol Modell **109**:61-75.

Sharpe, P. J. H., and D. W. DeMichele. 1977. Reaction-kinetics of poikilotherm development. Journal of Theoretical Biology **64**:649-670.

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

Webster, R. P., and R. T. Carde. 1982. Relationships among pheromone Titer, calling and age in the omnivorous leafroller moth (*Platynota stultana*). Journal of Insect Physiology **28**:925-933.

APPENDIX S2.- Description of the storage structure temperature survey

This appendix describes in detail the storage structure temperature survey performed to parameterize the storage structure scenario of our cellular automaton.

Methods

We located HOBO data-loggers (HOBO® U12 and Pro v2 U23-001 data-loggers, Onset Computer Corporation, Pocasset, MA, USA) inside and outside storage structures, fixed on a wooden stick at 1 m height from the ground in a shadow zone (for those that were outside). Temperatures were registered every 30 minutes for 6 different periods of 20 days between July 2007 and November 2008, in 6 storage structures located at different altitudes between 2700 and 3300 m. Relative humidity conditions were also surveyed but presented similar variation inside and outside (ranging between 60-85 %).

Results

We found that field temperatures were greatly buffered inside storage structures (Fig. 1).

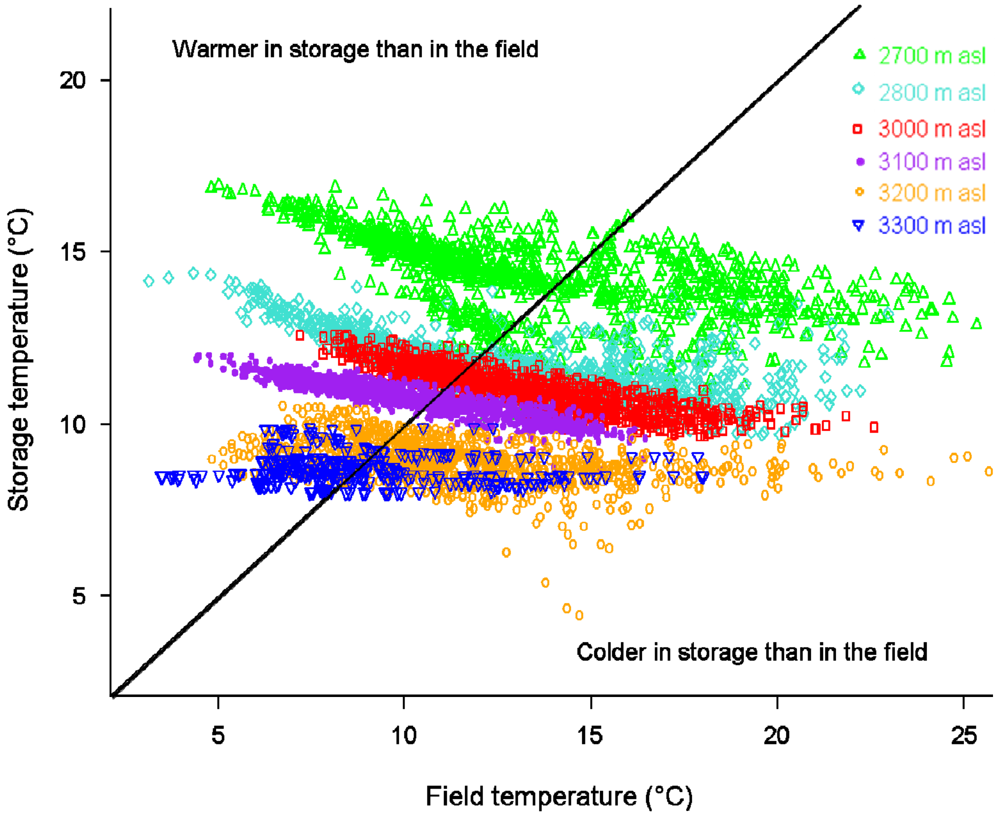


Fig.1. Relationship between storage structure and field temperatures at 6 sites located at different altitudes.

Whereas temperatures could vary to approximately 70-80 % of their median value in the field (often within the same day), their variation inside the storage structures was only c.a. 20-30 %. A similar buffer pattern inside the storage (negative linear model) was found at all sites whatever the altitude. These data imply that for a given altitude, there is a temperature threshold (intersection between the linear model and the 1:1 line) below which temperature is warmer inside the storage than in the field and above which it is colder.

To include these results into our model we separated the altitudinal range into groups of altitudes. For each group we adjusted a linear and three non-linear models (log, power and hyperbole). Since the linear model (eq. 2 of main text) showed the best overall performance we used it in our model to change the temperature of cells with storage structures as explained on the main text. Table 1 shows the values of the parameters of the linear model of each group of altitudes.

Table 1. Parameter values of the linear model relating temperatures inside and outside storage structures.

Altitude (m.a.s.l.)	*a*	*b*
2800 - 2899	-0.144	13.552
2900 - 2999	-0.144*	13.552*
3000 - 3099	-0.192	13.598
3100 - 3199	-0.183	12.636
3200 - 3299	-0.079	9.864
≥ 3300	-0.021	8.893

* Since the survey was not done at this altitudinal range we used the same parameters of the lower altitude range

CHAPTER 2

Modeling insect oviposition rate in heterogeneous thermal environments: insights from potato tuber moth in the tropical Andes

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

[1] IRD, UR 072, Diversité, Ecologie et Evolution des Insectes Tropicaux, Laboratoire Evolution, Génomes et Spéciation, UPR 9034, CNRS, 91198 Gif-sur- Yvette Cedex, France and Université Paris-Sud 11, 91405 Orsay Cedex, France

[2] Laboratorio de Entomología, Facultad de Ciencias Exactas y Naturales, Pontificia Universidad Católica del Ecuador, 12 de Octubre, 1076 y Roca, Quito, Ecuador

[3] Centre d'Ecologie Fonctionnelle et Evolutive, CNRS, 1919 route de Mende, 34293 Montpellier cedex 5, France

[4] Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, PO Box 10380 Stn. Ste Foy, Quebec, QC, Canada G1V 4C7

Corresponding auhtor: V. Crespo-Pérez, verocrespoperez@yahoo.com

Abstract

Oviposition is one of the main components of insects' fitness and population dynamics and is highly influenced by environmental temperature. Understanding the functional relationship between oviposition and temperature may help in the development of multigenerational population dynamics models which predictions are very useful in the deployment of more efficient pest control programs. Temperature variability is an important characteristic of landscapes, and accurate understanding of its influence on insects' dynamics could enhance robustness and realism of such models. In this contribution we modeled potato moth species' oviposition from data obtained at controlled constant temperatures and compared simulated oviposition under both constant and variable temperature regime. Our results show that the form of the temperature-related total oviposition curvediffers at constant and fluctuating temperatures. Total number of eggs was generally lower at optimal mean temperatures with fluctuating regimes and higher at extreme temperatures compared to constant regimes. Running our model with real temperature regimes obtained with data-loggers in the field and in potato storage structures at several sites in Ecuador revealed that the temperature buffering effect of storage structures is beneficial for moth oviposition at low altitudes, whereas it is detrimental at cold, high-altitude sites. We discuss our approach in light of similar approaches developed for other insects and mention possible implications of our results in a context of pest ecology under global change.

Key words

Fecundity, *Phthorimaea operculella*, Potato Tuber Moth, oviposition decay rate, oviposition modeling, temperature variability, *Symmetrischema tangolias, Tecia solanivora*

Introduction

Temperature profoundly affects behavior, physiology, and fitness of organisms (Angilletta 2009, Angilletta et al. 2010). Being ectotherms, insects' dynamics are strongly influenced by temperature of their environment. Precise information on insects' thermal responses helps predicting their phenology and distribution, a knowledge of great utility in the field of pest management (Régnière et al. 2009, Shea et al. 2010, Travis et al. 2011).

Oviposition is one of the main components of insects' fitness and population dynamics (Berger et al. 2008). It is highly influenced by temperature, although other abiotic and biotic factors, such as light intensity (Wyatt and Brown 1977), nutrition (Leather and Dixon 1982, Kaakeh and Dutcher 1993) and mating status (Steigenga and Fischer 2007) may confound its effects. Understanding the functional relationship between oviposition and temperature may help in the development of multigenerational phenology or population dynamics models.

Insects' responses to temperature may differ if exposed to constant or fluctuating temperature regimes (Gilchrist 1995, Gilbert et al. 2004, Davis et al. 2006, Adamo and Lovett 2011). Thus, insect population dynamics in highly variable environmental conditions may differ from those in more constant ones. This may be especially the case in environments, like the Tropical Andes, where temperatures tend to approach the physiological thresholds of insects (Dangles et al. 2008). Therefore, predictions of models based on insects response measured in constant temperatures may yield different and less realistic results from predictions of models that include the effect of temperature fluctuation on insect biology.

Potato cultures of the North Andean region are threatened by three species of Potato Tuber Moth (PTM), *Phthorimaea operculella* (Zeller), *Symmetrischema tangolias* (Gyen) and *Tecia solanivora* (Povolny), that have been invading the region for the past 30 years. Few attempts have been made to model these species dynamics (Sporleder et al. 2004, Dangles et al. 2008) and none have investigated the influence of the high levels of temperature variability characteristic of the region. The purpose of this study was to model these species' temperature-related oviposition. The model was parameterized with data obtained at controlled constant temperatures and used to simulate oviposition under constant and variable temperature regimes. This allowed us to predict the influence that temperature variability has on these species' oviposition dynamics.

Materials and Methods

Modeling oviposition

To model PTM oviposition rate we used data on temperature-related cumulative oviposition. For *P. operculella* we used data published by Sporleder et al. (2004, their Fig. 6a) who measured oviposition under seven constant temperautres (11, 15, 16, 20, 23, 26.2, 30 °C) . For the other two species we used oviposition data from several females raised at 12, 19 and 28 °C in climatic chambers (HACEB climatic chamber, Medellin, Colombia, for the trials at 12 °C and Memmert incubator, model INB-500, Schwabach, Germany, for those at 19 and 28 °C). Oviposition data for the three species is shown in Figure 1. We are not aware of any oviposition rate data obtained at fluctuating temperatures for these species (in fact they are non-existent for most 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 modeled oviposition following the approach developed by Régnière et al. (submitted). These authors considered that as females age and exhaust their reproductive resources, their daily oviposition rate declines, which causes cumulative oviposition to follow a diminishing return pattern. Each unit of time females lay a constant proportion, κ, of their remaining fecundity, F_t. This proportion may be a function of temperature κ(*T*,*B*), with *B* a set of parameters. Oviposition rate thus is:

$$\frac{dF_t}{dt} = -\kappa(T,B)F_t \tag{1}$$

In many species oviposition occurs after a pre-oviposition period, at time t_0, during which females mate and complete maturation. Solving (1) over time under constant temperature yields:

$$F_t = F_0 e^{-\kappa(T,B)(t-t_0)} \tag{2}$$

where F_0 is mean (potential) fecundity. Number of eggs laid accumulating from the onset of the oviposition period to time *t* is:

$$O_t = F_0\left(1 - e^{-\kappa(T,B)(t-t_0)}\right) \tag{3}$$

which produces the familiar diminishing return shape of most cumulative oviposition curves reported in the literature.

We used equation (3) to model *P. operculella* oviposition at each temperature. We fixed F_0 from our experimental data, and estimated the values of κ and t_0 by non-linear least squares using Microsoft Excel's Solver ®. In the case of *S. tangolias* and *T. solanivora*, for which we disposed of data for several females for each temperature treatment, we assumed a lognormal distribution of fecundities among individuals. The "lack of fit" between the theoretical oviposition rate at each temperature treatment j (eq. 3) and the actual oviposition of each individual i was termed δ_{ij} (with variance σ_δ^2). This lead to:

$$O_{ij} = \delta_{ij} F_0 \left(1 - e^{-\kappa(T,B)(t-t_0)}\right) \tag{4}$$

For these two species we used equation (4) to estimate F_0, σ_δ and κ through maximum likelihood, using Microsoft Excel's Solver ®, knowing that the probability of O_{ij} eggs being laid at temperature T from the onset of oviposition to time t is a lognormal cumulative density function of δ:

$$f\left(\delta_{ij}\right) = \frac{1}{\delta\sqrt{2\pi\sigma_\delta^2}} e^{-\frac{1}{2}x^2} \tag{5}$$

where $x = \left(\ln\left(\delta_{ij}\right) + \sigma_\delta^2 / 2\right) / \sigma_\delta$. The negative log likelihood to be minimized is:

$$LL = -\sum_i \sum_j \ln\left[f(\delta)\right] \tag{6}$$

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). We then examined the relationship between those parameter values and temperature. There was no clear relationship between pre-oviposition period and temperature. Thus, the value of t_0 was left as a single, temperature independent constant which corresponded to the mean pre-oviposition period across all temperatures.

Sporleder et al (2004; their Fig. 6b) approximated the relationship between F_0 and temperature by a second degree polynomial (three parameters). We chose to use a more flexible parabolic function with four parameters:

$$F_0 = a + bAbs\left|T - T_o\right|^x \tag{7}$$

where *a* is the maximum, *b* determines the width of the parabola, T_o is optimal temperature and *x* determines the flatness of the maximum. The addition of a fourth parameter allows a greater variety of parabolic shapes. Total fecundity data were adjusted to equation 3 through least sum of squares. In the case of *S. tangolias* and *T. solanivora* we adjusted this equation to published fecundity data (Notz 1995, Torres et al. 1997, Herrera 1998, Palacios et al. 1998, Álvarez and Trillos 1999, Castillo 2005) to obtain a general temperature-related fecundity curve for these species.

The relationship between κ and temperature was fitted to the Sharpe and DeMichele model modified by Schoolfield *et al.* (1981).

$$\kappa(T) = \frac{\rho_{25}\dfrac{T+273.15}{298.15}\exp\left[\dfrac{H_A}{1.987}\left(\dfrac{1}{298.15}-\dfrac{1}{T+273.15}\right)\right]}{1+\exp\left[\dfrac{H_L}{1.987}\left(\dfrac{1}{T_L}-\dfrac{1}{T+273.15}\right)\right]+\exp\left[\dfrac{H_H}{1.987}\left(\dfrac{1}{T_H}-\dfrac{1}{T+273.15}\right)\right]} \tag{8}$$

This model was developed to simulate temperature-dependent developmental rates and we used it to model PTM developmental rates (see Appendix S3 of this dissertation). In the case of *P. operculella* initial values of the model's six parameters were estimated by non-linear least squares with Microsoft Excel's Solver ®. For the other two species, since we only had three values for κ (at 12, 19 and 28 °C) we varied only parameters ρ_{25} and T_L and kept the others adjusted for *P. operculella*'s oviposition decay rate. Parameters were adjusted through non-linear least squares.

Finally, the full model was fitted to the entire datasets of each species:

$$O_t = \left[a + bAbs\left|T - T_o\right|^x\right]\left[1 - \mathbf{e}^{-\kappa(T,B)(t-t_0)}\right] \tag{9}$$

with $t > t_0$.

The 11 parameters of the full model (a, b, T_o, x, ρ_{25}, H_A, H_L, T_L, H_H, T_H and t_0) were estimated simultaneously by non-linear least-squares using Microsoft Excel's Solver ®.

Simulating oviposition under fluctuating temperatures

To understand how fluctuating temperatures influence female oviposition simulated by our approach we modeled PTM oviposition with a varying temperature regime. Equation (2) was used to determine oviposition rate over small time steps of Δt (fraction of a day). Because the time step is small temperature can be considered constant, so that:

$$E_{t-\Delta t,t} = O_t - O_{t-\Delta t} = F_0(T)\left[1-\mathbf{e}^{-\kappa(T,B)(t-t_0)}\right] - F_0(T)\left[1-\mathbf{e}^{-\kappa(T,B)(t-t_0-\Delta t)}\right] \tag{10}$$

which, rearranged algebraically gives:

$$E_{t-\Delta t,t} = F_0(T)\left[\mathbf{e}^{-\kappa(T,B)(t-t_0-\Delta t)} - \mathbf{e}^{-\kappa(T,B)(t-t_0)}\right] \tag{11}$$

Cumulative oviposition then, is:

$$O_t = \sum E_{t-\Delta t,t} \tag{12}$$

We ran simulations with a time step of $\Delta t = 0.2$ days, with temperature T fluctuating on a 24 h daily cycle along a sine curve, which is the rough pattern observed in the Ecuadorian sierra (see Dangles et al. 2008). We simulated moth oviposition for 250 time steps (i.e. 50 days, which corresponds to the maximum longevity observed for females raised in the laboratory). We examined the effect of regimes with several mean temperatures (8, 10, 12 14, 16, 18, 20, 22, and 24 °C), and with different levels of temperature variation (SD= 1, 5 and 10 °C), which resulted in 27 different scenarios (9 mean temperatures times three SD's). For each scenario we extracted values of F_0 and κ for each time-step, and the total oviposition, O_t, at the end of the simulation. This allowed comparing the variation of these variables among the different scenarios. We compared F_0 and κ across the different scenarios with a Kruskal-Wallis test and used a Mann-Whitney post-hoc analysis to compare pairs of scenarios.

Simulating oviposition under real temperatures

We were also interested in understanding the influence of actual temperature variation and of the temperature buffering effect of potato storage structures (Crespo-Pérez et al. accepted) on PTM oviposition dynamics. For this purpose, we simulated PTM oviposition under actual temperature regimes obtained from data-loggers' measurements over one year both in the field and inside potato storage structures at 3 different sites, located at three different altitudes (2700, 3000, 3300) in the Ecuadorian Andes.

As for the theoretical temperature regimes, we simulated moth oviposition for 250 time steps with each time step corresponding to 1/5 of a day. We also extracted the values of F_0 and κ for each time step and total oviposition, O_t, a at the end of the simulations, to compare their variation inside and outside the potato storage structures and among the different altitudes. We used a Kruskal-Wallis test and a Mann-Whitney post-hoc analysis to evaluate the differences in median values of the parameters between the different temperature regimes used for the simulations.

Results

Modeling oviposition under constant temperature regime

Fitting equation (3) to *P. operculella* data and (4) to *S. tangolias* and *T. solanivora*'s allowed us to model cumulative oviposition at several constant temperatures. Values of variables F_0, t_0, and κ (and σ_δ for *S. tangolias* and *T. solanivora*) for each species and temperature are shown in Table 1.

We used equation (7) to describe the three species' temperature-related total fecundity data. This allowed us to obtain bell-shaped curves, with optimal temperatures in the middle of the range and deleterious minimum and maximum temperatures (Fig. 2, and see Table 2 for parameter values). There was a high variability among the total fecundity data, especially among that of *T. solanivora*, for which the adjustment was less optimal ($R^2 = 0.75$) than that for the other two species' data ($R^2 = 0.89$ and 0.97 for *P. operculella* and *S. tangolias*, respectively).

Although values of κ of *P. operculella* provided no evidence of decay at high temperature, Sharpe and DeMichele's equation (modified by Schoolfield et al. 1981) allowed us to obtain upper threshold behavior at high temperatures without goodness-of-fit loss ($R^2 = 0.95$, Fig. 3, Table 2). The adjustment of this equation to *S. tangolias* and *T. solanivora*'s oviposition decay rate values was less optimal ($R^2 = 0.86$ and 0.59, respectively), but the resulting curves did present a high-temperature decay (Fig. 3, Table 2).

Cumulative oviposition predicted with equation (7) fitted well to observed cumulative oviposition of the three species obtained in laboratory at constant temperature (Fig. 4). Most of the error came from the variability in the relationship between F_0 and temperature.

Simulating oviposition under fluctuating temperatures

We found no clear pattern in the variation of F_0 among the different levels of temperature fluctuation and different mean temperatures (results not shown). Our results for the oviposition decay rate κ showed that increased level of fluctuation in temperature (i.e. increasing the standard deviation) produced a linear increase in the level of fluctuation of κ (i.e. its range) with $R^2 > 0.96$ for all mean temperatures for the three species. Box plots showing variation of κ across different levels of variation (SD= 1, 5 and 10) and with four different mean temperatures can be seen in Fig. 5. According to the Kruskall-Wallis analyses there were highly significant differences among the median values of κ of the oviposition scenarios tested within each species ($H = 967.5$, $P < 0.001$; $H = 967.6$, $P < 0.001$; $H = 1163$, $P < 0.001$, for *P. operculella*, *S. tangolias* and *T. solanivora*, respectively). Mann-Whitney pair-wise comparisons showed that for *P. operculella* and *S. tangolias,* SD “scenarios” within each mean temperature were not significantly different, whereas for *T. solanivora*, we found significant differences among the scenarios with mean temperatures of 12, 16 and 20 °C (Fig. 5).

As a general pattern, we found that median values of κ varied according to the shape of the temperature-related curves of κ (Fig. 3). In the case of *P. operculella*, where optimal temperature for κ (c.a. 36 °C) is far beyond the mean temperatures tested, this parameter showed a general increase with increasing mean temperature and larger ranges of values at higher temperatures (Fig. 5). In the other two species, in contrast, approaching optimal temperatures caused κ values to stabilize or to decrease. This was, for example the case for κ values for *T. solanivora* with mean temperatures of 16 and 20 °C, where large fluctuation in temperatures caused conditions to approach the suboptimal high temperature region for κ.

Comparing total fecundity O_t between the different levels of temperature fluctuation revealed that the relationship between oviposition and temperature changed when including fluctuating temperature regimes and varying the level of fluctuation (Fig. 6). For instance, with low levels of variation (SD = 1 °C) optimum temperature for *T. solanivora* was between c.a. 15 and 21 °C, whereas with a standard deviation of 5 °C the optimum temperature range became narrower (between c.a. 17 and 19 °C). Also, fluctuating temperatures caused *S. tangolias* total fecundity to decrease from 223 (with SD = 1 °C) to 82 eggs (with SD = 10 °C). In general, total fecundity tended to decrease and become somewhat constant with increasing levels of fluctuation. It is also important to note that in several cases oviposition near extreme high and low temperatures was higher in the regimes with higher temperature variation (i.e. SD = 5 and 10 °C) than that with lower variation (SD = 1 °C).

Simulating oviposition under real temperatures

We simulated moth oviposition with real temperature regimes from both the field and storage structures from three sites located at three different altitudes. This gave a total of six real temperature scenarios. We found no clear pattern in the variation of F_0 among the scenarios. Kruskal-Wallis analyses revealed significant differences in the oviposition decay rate among the different temperature regimes for the three species ($H = 796.7$, $P < 0.001$; $H = 796.7$, $P < 0.001$; $H = 796.9$, $P < 0.001$, for *P. operculella*, *S. tangolias* and *T. solanivora*, respectively). The variation in the decay rate was always higher in the field than inside the storage structures (Fig. 7), undoubtedly due to higher temperature variation in the former. We found a similar pattern in relation to altitude, where the level of variation in κ decreased with increasing altitude. Even though this high variation caused κ to often attain low values, it also allowed it to attain high values, which in the end, caused the mean values of κ to be higher in the field than inside the storage structures. Only in the case of *T. solanivora* at 2700 m.a.s.l. was κ, on average, higher in the storage structure than in the field.

The effect of the lower levels of temperature variability inside storage structures differed depending on the altitude considered. For instance, females of the three species were able to lay more eggs during their lifetime inside storage structures than in the field at 2700 m.a.s.l. (Fig. 8). At 3000 m.a.s.l., however, this pattern changed for *P. operculella* and *S. tangolias,* whose females laid more eggs in the field. Temperatures inside storage structures at 3300 m.a.s.l. were very low and hampered female oviposition almost completely, whereas in the field, females were able to lay some eggs probably because higher temperature variation in the field presented periods of higher temperatures that allowed some oviposition.

Discussion

Precise knowledge of temperature-related oviposition dynamics contributes to the development of accurate and realistic multigenerational phenological models (Sporleder et al. 2004). These models allow simulating insects' life history events both temporally and spatially and are powerful tools for efficient pest management programs (Régnière et al. 2009, Shea et al. 2010, Travis et al. 2011).

In spite of their importance as agricultural pests, potato tuber moth's population dynamics have been poorly studied and information on their temperature-related oviposition is scarce and incomplete (Notz 1995, Torres et al. 1997, Herrera 1998, Palacios et al. 1998, Sporleder et al. 2004). The approach used in this study allowed us to model PTM oviposition from laboratory data of females raised under constant temperatures. Our model was able to simulate the deleterious effect of extreme temperatures on fecundity already observed for females of *P. operculella* (Roux 1993, Sporleder et al. 2004) and of other insects (Kim and Lee 2003, Kuo et al. 2006). Accurately modeling insects' physiological responses near threshold temperatures is of prime importance if one wishes to enhance the precision and realism of the predictions, or if simulations are to be made with fluctuating temperature regimes (Régnière et al. submitted). This is especially important if one simulates processes in environments where temperature approaches extremes.

In this contribution, including the diminishing return pattern of cumulative oviposition allowed us to simulate PTM oviposition over time. A similar approach was used by Kim and Lee (2003) who employed a diminishing return type of function to model age-specific cumulative oviposition and combined it with temperature dependent total fecundity to model *Carposina sasakii*'s (Lepidoptera: Carposinidae) cumulative oviposition. Such approaches are useful for simulating oviposition over consecutive time-steps, and the non-linearity of the diminishing return curves allows realistic predictions near threshold temperatures (Kim and Lee 2003).

Temperature variability strongly influences poikilotherms population dynamics (Gilchrist 1995, Gilbert et al. 2004, Davis et al. 2006, Adamo and Lovett 2011). Models capable of simulating those dynamics under fluctuating temperatures are thus very useful. Gilbert et al. (2004) compared three different models to simulate Mountain Pine Beetle development and highlighted the ability of one of those models (the Extended von Foerster model) to realistically model development under varying temperatures.

The approach presented in this contribution allowed us to simulate PTM daily oviposition under fluctuating temperature regimes and to understand the influence of temperature variability on oviposition dynamics. Our results showed that simulated oviposition dynamics at fluctuating temperatures greatly differed from those at constant temperatures. We found, for instance, that fluctuating temperatures sometimes produce changes in the optimal temperature range for maximum oviposition and may allow a higher number of eggs to be laid at temperature extremes. This result is in agreement with results found by Davis et al. (2006) for the green peach aphid *Myzus persicae* and by Adamo and Lovett (2011) for the cricket *Gryllus texensis* who found that fluctuating temperatures allow or enhance process rates like development, survival and reproduction at high mean temperatures, where these processes are hampered at constant temperature regimes.

Thorough understanding of the influence of temperature fluctuation on insects' dynamics is of extreme importance in highly variable environments, like the tropical Andes, where daily temperature variations are higher than annual variations (Dangles et al. 2008). High human activity in this region, and the consequent increase of human constructions that buffer field temperatures, requires precise knowledge of the differences in population dynamics between stable and unstable environments. Our study showed that the influence of storage structures on PTM oviposition varied depending on the altitude and on the species considered. Our results confirmed those of Keller (2003), who based on farmer interviews, found that some high altitude stores at the Mantaro Valley (central Peru) were less infested by the potato tuber moth, *Symmetrischema tangolias*, than lower altitude stores, probably due to the constant low temperatures inside the former. Accurate descriptions of insects' dynamics in relation to temperature and its variation are also of primary importance in a climate change context. Climate change models predict that in the future organisms will be subject not only to higher temperatures but also to larger temperature variability (IPCC 2007).

This study constitutes a novel and interesting approach to modeling oviposition in heterogeneous environments and presents interesting insights on the influence of such heterogeneity on oviposition dynamics. However, results remain theoretical since they have not been validated with actual data of moth oviposition in fluctuating temperature regime. We are not aware of the existence of such data for PTM. A way of testing this modeling approach could be to collect data on moth oviposition dynamics inside and outside potato storage structures and compare those results to our simulations.

Acknowledgments

This work was part of the research conducted within the project *Innovative Approaches for integrated Pest Management in changing Andes* (C09-031) funded by the McKnight Foundation. This work was part of VCP's doctoral project, financed by grants from the French Embassy in Ecuador and from the *Département Soutien et Formation des communautés scientifiques du Sud* (DSF) of the IRD. We thank Mario Herrera for his help with lab work.

References

Adamo, S. A., and M. M. E. Lovett. 2011. Some like it hot: the effects of climate change on reproduction, immune function and disease resistance in the cricket *Gryllus texensis*. Journal of Experimental Biology **214**:1997-2004.

Álvarez, G., and O. Trillos. 1999. Estudio sobre la Biología y Cría de la Polilla de la Papa *Tecia solanivora* Povolny. Plan Estratégico para el Manejo de *Tecia solanivora* en Colombia. Ministerio de Agricultura y Desarrollo Rural Universidad Nacional de Colombia, Bogota.

Angilletta, M. J. 2009. Thermal Adaptation: a theoretical and empirical synthesis. Oxford University Press, New York.

Angilletta, M. J., R. B. Huey, and M. R. Frazier. 2010. Thermodynamic Effects on Organismal Performance: Is Hotter Better? Physiological and Biochemical Zoology **83**:197-206.

Berger, D., R. Walters, and K. Gotthard. 2008. What limits insect fecundity? Body size- and temperature-dependent egg maturation and oviposition in a butterfly. Functional Ecology **22**:523-529.

Castillo, G. M. 2005. Determinación del ciclo de vida de las polillas de la papa *Symmetrischema tangolias* (Gyen) y *Tecia solanivora* (Povolny) bajo condiciones controladas de laboratorio. Universidad Central del Ecuador, Quito.

Crespo-Pérez, V., F. Rebaudo, J.-F. Silvain, and O. Dangles. accepted. Modeling invasive species spread in complex landscapes: the case of potato moth in Ecuador. Landscape Ecology.

Dangles, O., C. Carpio, A. R. Barragan, J. L. Zeddam, and J. F. Silvain. 2008. Temperature as a key driver of ecological sorting among invasive pest species in the tropical Andes. Ecol Appl **18**:1795-1809.

Davis, J. A., E. B. Radcliffe, and D. W. Ragsdale. 2006. Effects of high and fluctuating temperatures on *Myzus persicae* (Hemiptera : Aphididae). Environmental Entomology **35**:1461-1468.

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

Gilchrist, G. W. 1995. Specialists and Generalists in Changing Environments .1. Fitness Landscapes of Thermal Sensitivity. American Naturalist **146**:252-270.

Herrera, F. 1998. La polilla guatemalteca de la papa: biología, comportamiento y prácticas de manejo integrado. Corporación Colombiana de Investigación Agropecuaria (CORPOICA), Bogotá, Colombia.

IPCC. 2007. Working group I report, climate change 2007: ‘‘the physical science basis’’. Paris.

Kaakeh, W., and J. D. Dutcher. 1993. Rates of increase and probing behaviour of *Acyrthosiphon pisum* (Homoptera, Aphididae) on preferred and nonpreferred host cover crops. Environmental Entomology **22**:1016-1021.

Keller, S. 2003. Integrated Pest Management of the Potato Tuber Moth in Cropping Systems of Different Agroecological Zones. Margraf Publishers, Germany.

Kim, D. S., and J. H. Lee. 2003. Oviposition model of *Carposina sasakii* (Lepidoptera : Carposinidae). Ecological Modelling **162**:145-153.

Kuo, M. H., M. C. Chiu, and J. J. Perng. 2006. Temperature effects on life history traits of the corn leaf aphid, *Rhopalosiphum maidis* (Homoptera : Aphididae) on corn in Taiwan. Applied Entomology and Zoology **41**:171-177.

Leather, S. R., and A. F. G. Dixon. 1982. Secondary host preferences and reproductive activity of the bird cherry-oat aphid, *Rhopalosiphum padi*. Annals of Applied Biology **101**:219-228.

Notz, A. 1995. Influencia de la temperatura sobre la biologia de *Tecia solanivora* (Povolny) (Lepidoptera: Gelechiidae) criadas en tuberculos de papa *Solanum tuberosum* L. Boletín de Entomología Venezolana **11**:49-54.

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

Régnière, J., V. Nealis, and K. Porter. 2009. Climate suitability and management of the gypsy moth invasion into Canada. Biol Invasions **11**:135-148.

Régnière, J., J. Powell, B. Bentz, and V. Nealis. submitted. Temperature responses of insects: design of experiments, data analysis and modeling. Ecologica Applications.

Roux, O. 1993. Population ecology of potato tuber moth *Phthorimaea operculella* (Zeller) (Lepidoptera:Gelechiidae) and design of an integrated pest management program in Tunisia. SWISS FEDERAL INSTITUTE OF TECHNOLOGY, Zurich.

Schoolfield, R. M., P. J. H. Sharpe, and C. E. Magnuson. 1981. Non-Linear Regression of Biological Temperature-Dependent Rate Models Based on Absolute Reaction-Rate Theory. Journal of Theoretical Biology **88**:719-731.

Shea, K., E. Jongejans, O. Skarpaas, D. Kelly, and A. W. Sheppard. 2010. Optimal management strategies to control local population growth or population spread may not be the same. Ecological Applications **20**:1148-1161.

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

Steigenga, M. J., and K. Fischer. 2007. Ovarian dynamics, egg size, and egg number in relation to temperature and mating status in a butterfly. Entomologia Experimentalis Et Applicata **125**:195-203.

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

Travis, J. M. J., C. M. Harris, K. J. Park, and J. M. Bullock. 2011. Improving prediction and management of range expansions by combining analytical and individual-based modelling approaches. Methods in Ecology and Evolution:no-no.

Wyatt, I. J., and S. J. Brown. 1977. Influence of light intensity, daylength and temperature on increase rates of 4 glasshouse aphids. Journal of Applied Ecology **14**:391-399.

Tables

Table 1. Values of F_0, t_0, and κ for each species and temperature adjusted with equation (3) for *P. operculella* and equation (4) for *S. tangolias* and *T. solanivora*.

P. operculella					*S. tangolias*						*T. solanivora*					
Temp (°C)	F_0	a_0	κ	r^2	Temp (°C)	F_0	a_0	κ	σ_δ	-LL	Temp (°C)	F_0	a_0	κ	σ_δ	-LL
11	72.90	0.72	0.11	0.99	12	150.00	0.90	0.05	0.45	40.14	12	250.00	1.00	0.10	0.78	128.18
15	158.10	0.00	0.16	0.99	19	130.00	0.00	0.17	0.24	-6.67	19	183.53	0.27	0.20	0.23	-7.538
16	131.70	0.00	0.14	0.99	28	5.00	0.99	0.20	0.40	55.81	28	13.00	0.01	0.15	0.84	13.871
20	145.70	0.83	0.27	0.99												
23	180.30	0.58	0.35	0.98												
26.2	150.20	0.89	0.34	0.99												
30	72.50	0.45	0.47	0.98												

Table 2. Parameter estimates of the oviposition model for the three species.

Parameter	*P. operculella*	*S. tangolias*	*T. solanivora*
T_o	20.513	15.583	18.14837
a	151.704	229.363	291.982
b	-0.002	-8.434	-0.001
x	4.706	1.769	6.200
a_0	0.515	0.004	0.455
ρ_{25}	0.416	0.690	0.580
H_A	15355.96	15355.96	15355.96
H_L	-59927.9	-59927.9	-59927.9
T_L	256.628	256.628	256.628
H_H	30000.01	30000.01	30000.01
T_H	309.43	309.43	309.43

Figure captions

Fig. 1. Observed cumulative oviposition at different constant temperatures. Data for *P. operculella* come from Sporleder et al. (2004) and for the other two species from experiments performed at our laboratory.

Fig. 2. Relationship between total fecundity and temperature, adjusted with equation 7. Total fecundity data for *P. operculella* come from Sporleder et al. (2004), and for the other 2 species from various literature sources (Notz 1995, Torres et al. 1997, Herrera 1998, Palacios et al. 1998, Álvarez and Trillos 1999, Castillo 2005).

Fig. 3. Relationship between predicted oviposition decay rate (κ) and temperature, adjusted to the Sharpe and DeMichel model.

Fig. 4. Predicted versus observed cumulative oviposition. The graphs group cumulative oviposition data obtained at 7 different temperatures for *P. operculella* and three for *S. tangolias* and *T. solanivora*.

Fig. 5. Variation of the predicted oviposition decay rate (κ) under fluctuating temperature regimes with different levels of variation (SD= 1, 5 and 10) and four different mean temperatures.

Fig. 6. Predicted total fecundity of females of the three species under fluctuating temperature regimes with different levels of variation and several mean temperatures.

Fig. 7. Predicted oviposition decay rate (κ) under actual temperature regimes inside potato storage structures and in potato fields at three sites located at different altitudes in the Ecuadorian Andes.

Fig. 8. Predicted total fecundity under actual temperature regimes inside potato storage structures and in potato fields at three sites located at different altitudes in the Ecuadorian Andes.

Figures

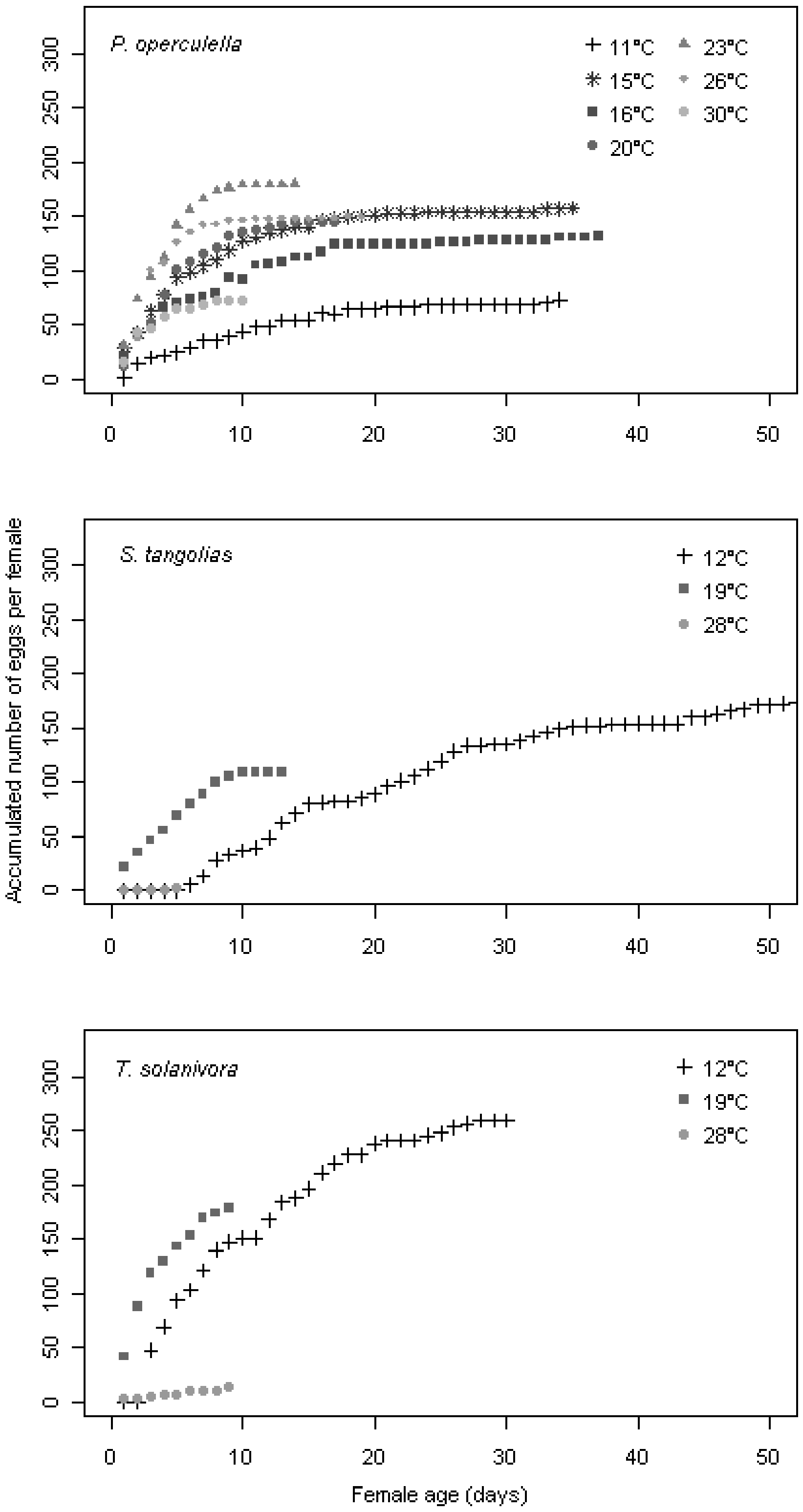


Fig. 1.

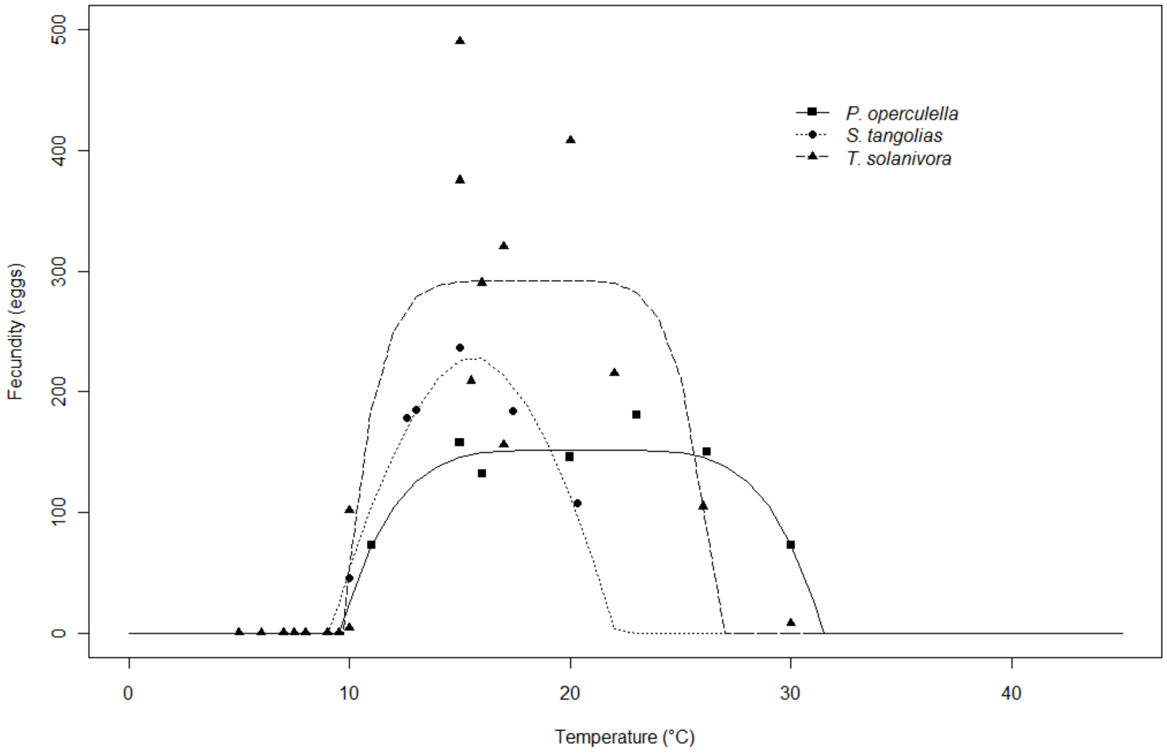
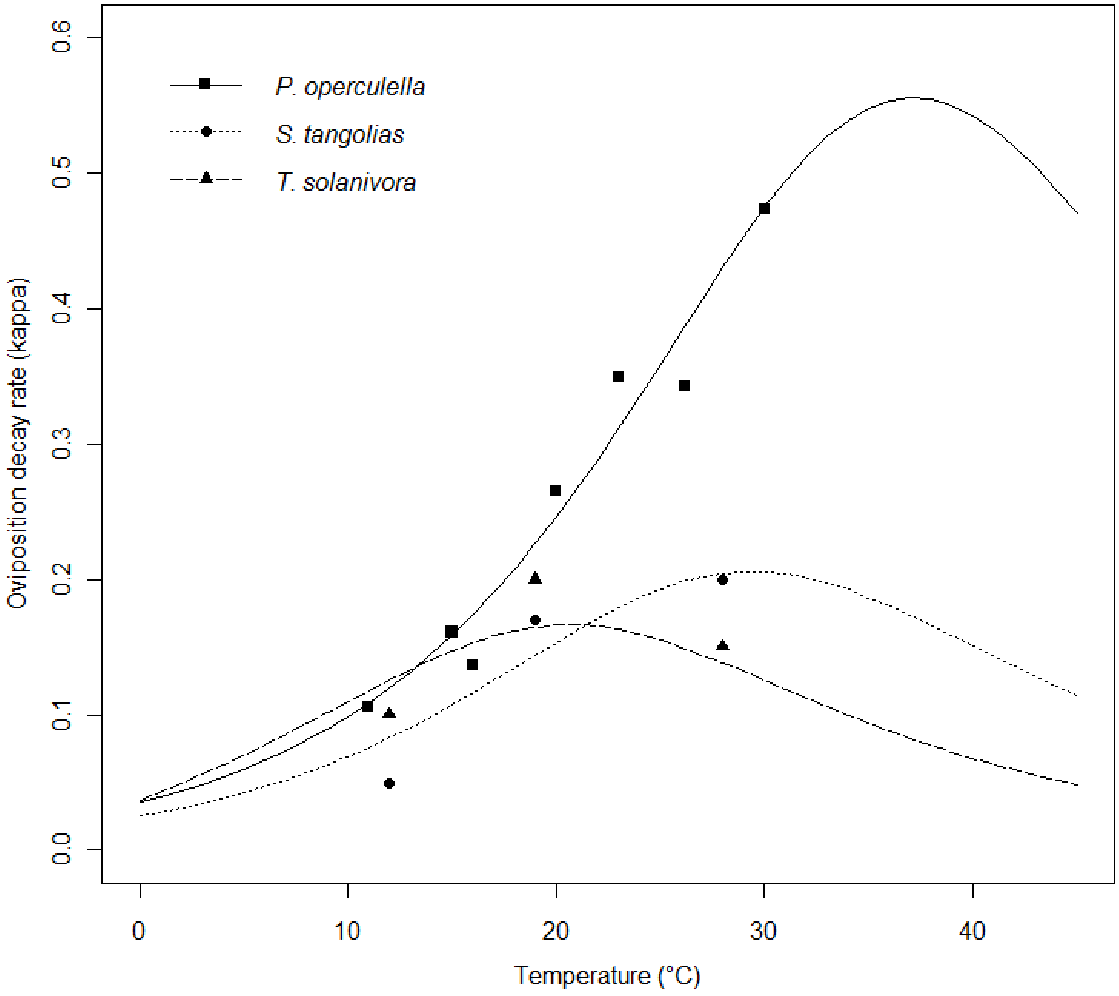

P. operculella
S. tangolias
T. solanivora
Fecundity (eggs)
0
100
200
300
400
500
0
10
20
30
40
Temperature (°C)

Fig. 2.



P. operculella
S. tangolias
T. solanivora
Oviposition decay rate (kappa)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0
10
20
30
40
Temperature (°C)

Fig. 3.

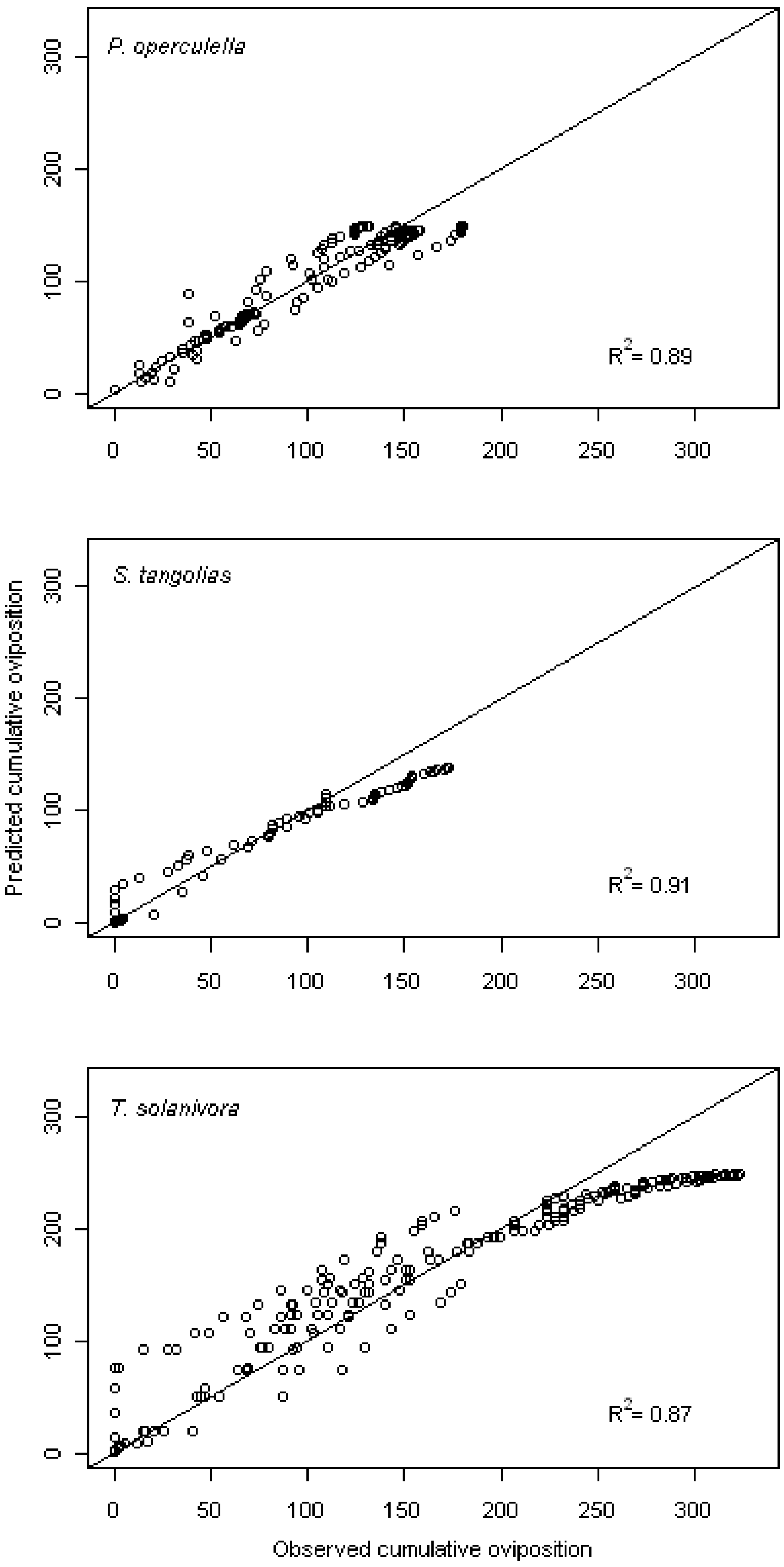

P. operculella
R² = 0.89
S. tangolias
R² = 0.91
T. solanivora
R² = 0.87
Predicted cumulative oviposition
Observed cumulative oviposition
0
100
200
300
0
50
100
150
200
250
300

Fig. 4.

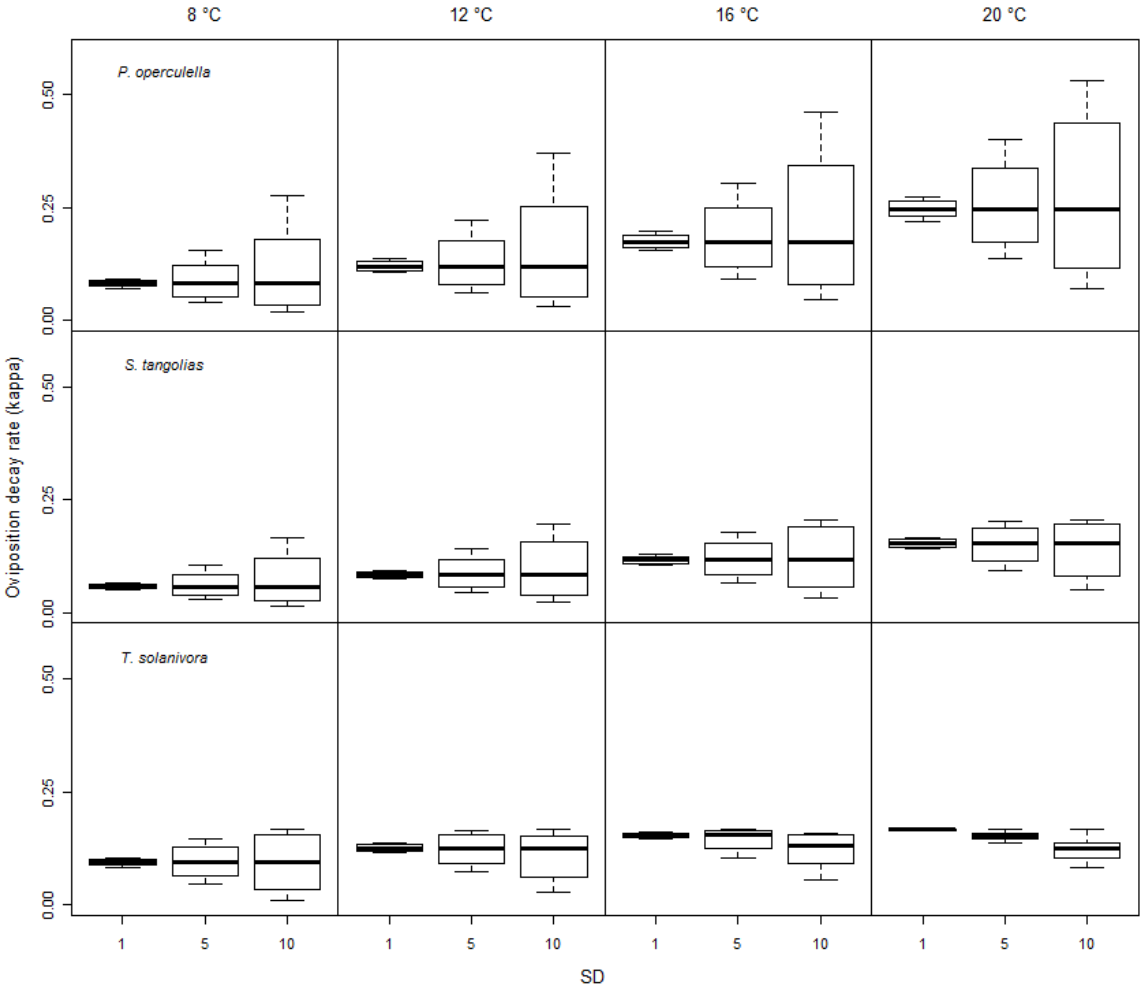

8 °C
12 °C
16 °C
20 °C
P. operculella
S. tangolias
T. solanivora
Oviposition decay rate (kappa)
0.00
0.25
0.50
1
5
10
SD

Fig. 5.

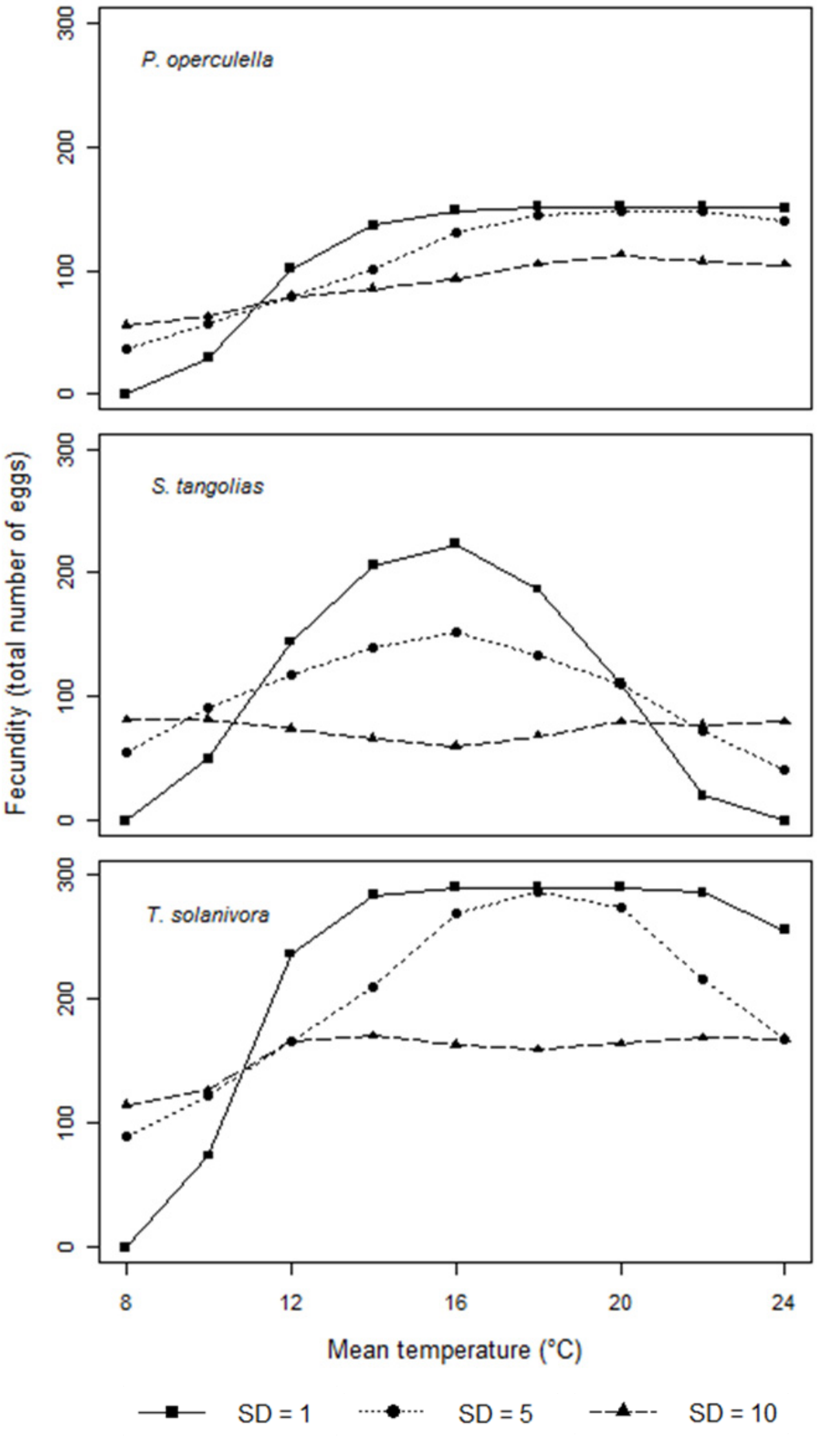

P. operculella
S. tangolias
T. solanivora
Fecundity (total number of eggs)
0
100
200
300
8
12
16
20
24
Mean temperature (°C)
SD = 1
SD = 5
SD = 10

Fig. 6.

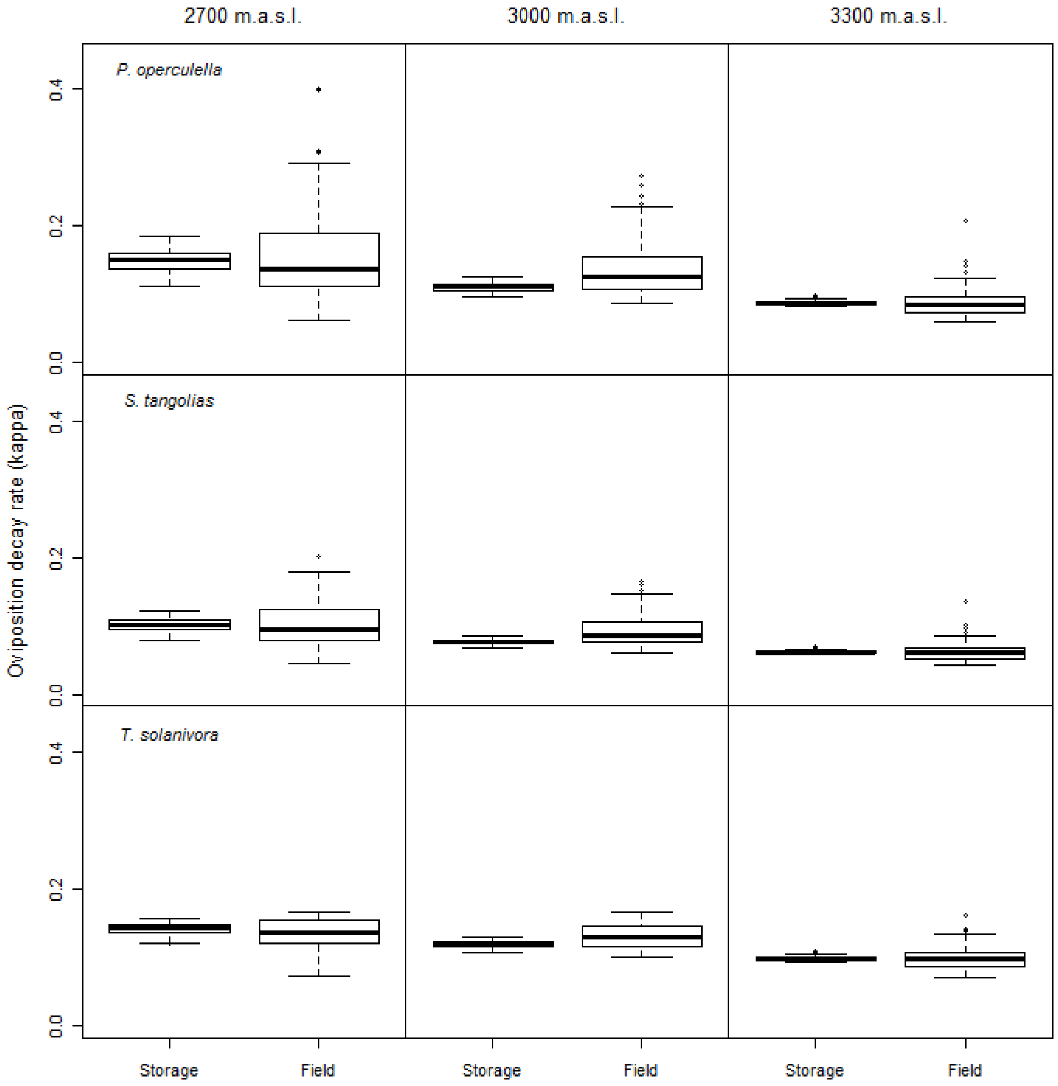

2700 m.a.s.l.
3000 m.a.s.l.
3300 m.a.s.l.
P. operculella
S. tangolias
T. solanivora
Oviposition decay rate (kappa)
0.0
0.2
0.4
Storage
Field

Fig. 7.

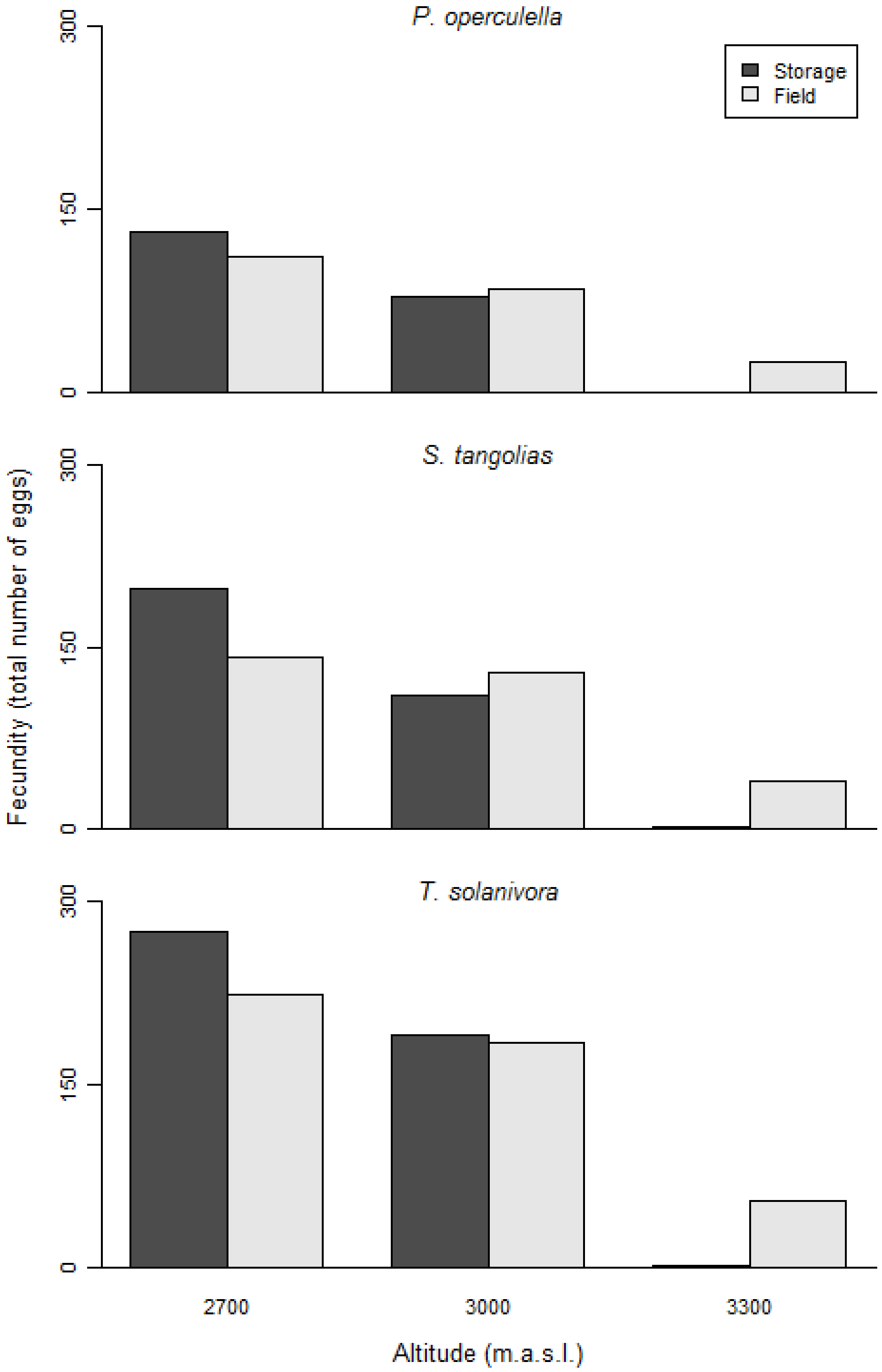

P. operculella
Storage
Field
S. tangolias
T. solanivora
Fecundity (total number of eggs)
0
150
300
2700
3000
3300
Altitude (m.a.s.l.)

Fig. 8.

CHAPTER 3

Modeling temperature-dependent survival with small data sets: Insights from potato pests in the tropical Andes

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

[1] IRD, UR 072, Diversité, Ecologie et Evolution des Insectes Tropicaux, Laboratoire Evolution, Génomes et Spéciation, UPR 9034, CNRS, 91198 Gif-sur- Yvette Cedex, France and Université Paris-Sud 11, 91405 Orsay Cedex, France

[2] Laboratorio de Entomología, Facultad de Ciencias Exactas y Naturales, Pontificia Universidad Católica del Ecuador, 12 de Octubre, 1076 y Roca, Quito, Ecuador

[3] Centre d'Ecologie Fonctionnelle et Evolutive, CNRS, 1919 route de Mende, 34293 Montpellier cedex 5, France

[4] Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, PO Box 10380 Stn. Ste Foy, Quebec, QC, Canada G1V 4C7

Corresponding author: V. Crespo-Pérez, verocrespoperez@yahoo.com

Abstract

Survival probability is an important component of fitness. Insect survival is mainly influenced by temperature and is commonly modeled with tolerance curves which allow the identification of favorable sites for pest establishment. They are therefore useful tools within insect pest management programs. The tropical Andes are increasingly threatened by agricultural pests but studies and data on their temperature-related dynamics are scarce. This hampers the development of adequate population dynamics models that could potentially contribute to pest management strategies. Here we present a new model relating survival to temperature and compare its performance to two published models. We adjusted the models to survival data of three species of potato tuber moth (PTM), some major pests in the region. We were particularly interested in their ability to simulate the deleterious effect of extreme temperatures even when adjusted to a dataset that did not include extreme temperature conditions. To evaluate model performance we considered both goodness-of-fit and robustness. The latter consisted in evaluating their ability to generate the parabolic shape characteristic of temperature related survival with high mortality at extreme temperatures and to predict the actual altitudinal limits of the species in the Ecuadorian Andes. We found that even though our model did not always provide the best fit to the data, it predicted extreme temperature mortality and altitudinal limits better than the other two models and with a very good accuracy. Our study shows that the ability to accurately represent the physiological limits of species is important to provide robust predictions of invasive pests' potential distribution, particularly in places where temperatures approach lethal extremes. The value of the model presented here lies in its ability to simulate accurate thermal tolerance curves even with small data sets, which is useful in places like the Tropical Andes (and probably in other tropical regions), where adequate pest management is urgent but data are scarce.

Key words

Agricultural pests, *Phthorimaea operculella*, Potato Tuber Moth, *Symmetrischema tangolias*, *Tecia solanivora*, temperature-related survival

Introduction

A species' fitness in a particular ecosystem depends on its responses to environmental conditions (Gilchrist 1995). Survival probability reflects the level of tolerance of organisms to the environment and is an important component of fitness (Huey and Kingsolver 1989, Gilchrist 1995). The survival of ectotherms, such as insects, is mainly influenced by temperature (Drost et al. 1998) and occurs within a definite temperature range, with an optimum between high and low lethal temperatures (Janisch 1932, Price 1997, Angilletta et al. 2002, Angilletta 2009). Temperature-related survival in insects is commonly modeled with tolerance curves, which are functions that describe survival rate along a temperature continuum (Gilchrist 1995). Determining such tolerance curves is useful within insect pest management programs since they allow the identification of vulnerable sites when coupled to temperature regimes that occur in a particular landscape (Logan and Powell 2001, Logan et al. 2007).

Most studies of temperature-dependent process rates in insect pests come from temperate regions (Régnière and Sharov 1998, Régnière and Bentz 2007). Tropical regions, in particular mountainous ones have received much less attention although they represent important places for agriculture development. These regions are characterized by an unmarked seasonality and high environmental heterogeneity along the altitudinal gradient (Dangles et al. 2008). This, along with high levels of human activities mostly related to agriculture (Nyssen et al. 2009), allows pests to thrive and propagate causing considerable losses in developing countries (Dangles et al. 2010). These regions are thus in urgent need of accurate and efficient risk assessment tools that will allow governments to focus their management effort on the most vulnerable sites (Perez et al. 2010). However, the lack of data on dynamics of many pest species threatening agricultural landscapes in the tropics often hinders the development of adequate pest dynamics models needed for pest risk assessment.

The objective of this study was to compare the performance of three models to simulate the temperature-related survival of the three immature stages (eggs, larvae, and pupae) of the three species of potato tuber moth (PTM), *Phtorimaea operculella* (Zeller), *Symmetrischema tangolias* (Gyen), and *Tecia solanivora* (Povolny), that are serious pests of potatoes in the Northern Andean region (Dangles et al. 2010). Data on extreme lethal temperatures are seldom available and their absence is often a drawback for accurate modeling of species survival rate. In this work we evaluated the ability of various models to predict the deleterious effect of temperature even when adjusted to a dataset that does not include data on lethal temperatures. Accurately estimating lethal temperatures is important in places where temperatures may approach such levels. High altitude sites in the tropical Andes, for example, present low mean temperatures that may reduce the pests' survival and thus restrict their distribution (Sporleder et al. 2004).

The first model we tested was the Sharpe and DeMichele's model (Sharpe and DeMichele 1977, modified by Schoolfield et al. 1981) originally developed to describe poikilotherm development rate. Although widely used to model ectotherm development, in particular that of the PTM *P. operculella*, its large number of parameters may be difficult to estimate when fitted to a small number of data points not covering a wide range of temperatures. The second model we evaluated was a second order polynomial function used by Sporleder et al. (2004) to describe mortality rate of *P. operculella*. Even though these authors managed to adjust this model fairly well to their data this model may fail to produce the bell shaped form typical of survival curve. Finally, we tested the performance of a model developed by Régnière et al. (submitted). This model considers the effect of temperature on survival rate in conjunction with development time, both determining the overall temperature related survival.

Materials and methods

Potato tuber moths

Within the last 30 years *Phtorimaea operculella* (Zeller), *Symmetrischema tangolias* (Gyen), and *Tecia solanivora* (Povolny) have been invading the potato fields of the Northern Andes and represent today one of the most serious agricultural pest problems in the region (Dangles et al. 2010). Undoubtedly due to its worldwide distribution, *P. operculella* has been the most studied (Rondon 2010). In the Northern Andes the three species have been observed co-occurring in some places, even within the same potato storage structure or sack (Dangles et al. 2008). Although little is known about their interaction, controlled laboratory experiments report either competition or facilitation between them, depending on the temperature and on the sequence of introduction (Dangles et al. 2009). The degree of damage to field or stored potato thus depends on which species are present and on the sequence of invasion.

Furthermore, since they have proven to respond differently to control strategies (for instance to a given granulovirus isolate used for biological control, Sporleder et al. 2005, Rebaudo et al. 2006), their coexistence may complicate the establishment and success of control tactics. These three species seem to differ in their physiological responses to temperature (Dangles et al. 2008), which play an essential role in defining their geographic distribution along the highly environmentally heterogeneous Northern Andean landscapes. Therefore, integrated pest management of these pests will greatly benefit from a thorough understanding of their thermal niches.

Data compilation

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

Modeling survival

Temperature-related survival has been shown to have a parabolic shape, with low survival at low and high temperatures (van der Have 2002). In this study, we assess the convenience of three different models for simulating temperature related survival.

1) Sharpe and DeMichele's model

This model was developed by Sharpe and DeMichele (1977) to describe the kinetics of insect development based on several assumptions about the underlying developmental control enzymes. It has been widely used to describe poikilotherms' temperature- dependent development (Gilbert et al. 2004). We decided to include Sharpe and DeMichele's model (as modified by Schoolfield et al. 1981) in our study because of its biological significance and because it has been successfully used to simulate tuber moth development and survival in other studies (Roux 1993, Sporleder et al. 2004). The equation of survival is:

$$P(survival) = \frac{\frac{dT}{298.16}\exp(\frac{1}{298.16} - \frac{1}{T})}{1 + \exp[\frac{f}{R}(\frac{1}{g} - \frac{1}{T})] + \exp[\frac{h}{R}(\frac{1}{i} - \frac{1}{T})]} \tag{1}$$

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

2) Sporleder's polynomial model

Sporleder et al. (2004) used a second order polynomial function of the form:

$$M(T) = m_1T^2 + m_2T + i, \tag{2}$$

to describe the relation between mortality rate $M(T)$ and temperature for the different life stages of the *P. operculella*. m_1, m_2 and i are parameters to be estimated (see *Models' parameterization* section bellow). While second degree polynomials are appropriate to describe a parabolic relationship they usually provide a poor extrapolation beyond the range of observations. Nevertheless, we decided to test this rather simple model on survival data of the three species of PTM since it had already been used to simulate mortality of one of the species of PTM (Sporleder et al. 2004). To model our survival data we expressed survival rate as the inverse of mortality rate: $P(survival) = 1 - M(T)$.

3) Régnière's model

Régnière et al. (submitted) assume that the probability of survival at a given temperature is constant from day to day, and that overall survival is simply a matter of exposure duration to that daily survival probability. Under these conditions, the probability of survival over the duration of a given life stage at temperature T is:

$$P(survival) = s^{t(T)} \tag{3}$$

Where t is development time at temperature T (see Appendix S3 for a description of the functions relating development time to temperature for each species and stage), and s the survival rate at a given temperature T, which is assumed to be a function of T, $s(T)$. Through the transformation:

$$Logit(s) = \ln[s/(1-s)] \quad (4)$$

the existence of a relationship between daily survival rate and temperature can be tested with a simple polynomial (parabolic) model of the form:

$$Logit(s) = a + bT + cT^2 \quad (5)$$

Returning to the normal scale gives:

$$P(survival) = \left(\frac{e^{a+bT+cT^2}}{1+e^{a+bT+cT^2}} \right)^{t(T)} \quad (6)$$

with a, b and c parameters to be estimated.

Models' parameterization

Parameters of the three models were estimated using log-likelihood assuming that the number of survivors out of the initial number in each treatment is binomially-distributed, with probability P(survival). In the case of *S. tangolias*, for which we did not dispose of data on initial number of moths and hence on number of survivors for part of the survival data, we adjusted parameters using least sum of squares.

Model performance evaluation

We used the Bayesian Information Criterion (BIC) (Schwarz 1978), to compare the performance of the three models:

$$\text{BIC} = (-2 * LL) + (k * \text{Ln}(n)) \quad (7)$$

where *LL* is log-likelihood of the model, *k* is the number of parameters in the model, and *n* is sample size (i.e. number of data points). The model that had the smallest value of BIC was considered the best. In the case of the models fitted to *S. tangolias* data, that were fitted using least squares, we calculated BIC with the following equation:

$$\mathrm{BIC} = n * \ln(RSS/n) + \ln(n) * k$$

where *RSS* is the residual sum of squares of the model.

Additionally, we assessed the models' robustness in two ways. First we evaluated their ability to generate the parabolic shape characteristic of temperature related survival with high mortality at extreme temperatures (Angilletta 2009), in spite of data points used for the model fit being only from the middle of the temperature range. Second, we evaluated the ability of models to predict the actual altitudinal limits of the species. For this, we first calculated with the three models the probability of survival of each immature life stage of each species in the Ecuadorian Andes (altitudes over 2000 m.a.s.l., where potato culture begins in Ecuador) using WorldClim mean yearly temperature (with a resolution of 1 km^2), using the "Map Algebra" tool from ArcMap. To obtain the survival of each species, we multiplied the survival rates of eggs, larvae, and pupae for each of them.

Then we computed the survival probability predicted by the three models at the altitude of 50 field sites were moth abundance has been regularly monitored by our team between 2006 and 2008. Subsequently we adjusted linear models to the relationships between survival probability and altitude. Finally, predicted survival probabilities along the altitudinal gradient were compared to the observed altitudinal limits of the three species (Dangles et al. 2008). Predicted survival probability was also compared to observed abundance While we are aware that species may not be at equilibrium with the environment and have probably not yet filled their potential range, the current altitudinal limits of the species is probably close to the equilibrium with climate and might be explained by survival probability due to major thermal-related physiological constraints (Dangles et al. 2008).

Results

Model fit

The three models used to describe the temperature related survival data of the immature stages of *P. operculella*, *S. tangolias*, and *T. solanivora* present similar performances (i.e. there is little variation between the values of BIC among the three models for each stage of each species) (Table 2). The BIC shows that Sporleder's parabolic model is most often the one that best explains the data relative to its number of parameters (Table 2). Régnière's model has the lowest BIC for *P. operculella* eggs and pupae, and *S. tangolias* eggs' survival. Sharpe and DeMichel's model has the lowest BIC only for *T. solanivora* pupae (Table 2).

In most cases, the three models are able to simulate the decay in survival rate at low and high temperatures and optimal survival at mid-temperatures (Fig. 1), but they often differ in their predictions of the optimal temperature and the high and low lethal temperatures. Sporleder's polynomial model is unable to produce parabolas when adjusted to data of *P. operculella* eggs and *T. solanivora* pupae (Fig 1a and 1i) where it predicts high survival all along the temperature range. In contrast, both Régnière's and Sharpe and DeMichele's models produce bell shaped curves for those stages of those species. Survival probability at low temperatures predicted by both Sporleder's and Sharpe and DeMichel's models are higher in some cases than that predicted by Régnière's model (i.e. Fig 1c, e and i) and Sporleder's model predicts close to 100 % survival of *T. solanivora* pupae at 0 °C (Fig. 1i). Regnière's model always succeeds in predicting 0% survival at low and high temperatures contrary to Sporleder and Sharpe and DeMichel's models.

Prediction of moth distribution

Simulations with the models using the mean annual temperature (with temperature comprised between -5.6 °C and 23.6 °C) allowed us to predict survival probability of the three species over the Ecuadorian Andes. Differences in survival lie mostly at high and low altitudes, with fewer differences at mid-altitudes (Fig. 2). As a general pattern, PTM present a higher survival at valleys located in the center of the Andes and on both sides of the mountain chain where temperatures are higher.

P. operculella's survival probability is best described by a linear model of altitude, ($S = ax + b$, with S representing survival probability and x altitude in m.a.s.l., and $R^2 = 0.57$, 0.56, and 0.42 for predictions by Sharpe and DeMichele's, Sporleder's, and Régnière's models, respectively). *S. tangolias'* survival probability is best described by a cubic model of altitude ($S = ax^3 + b$, R^2 of 0.57, 0.61, and 0.57 for Sharpe and DeMichele's, Sporleder's, and Régnière's models, respectively). *T. solanivora*'s survival probability is best described by a second order polynom of altitude ($S = ax^2 + bx + c$, $R^2 = 0.56$, 0.56, and 0.58 for Sharpe and DeMichele's, Sporleder's, and Régnière's models, respectively). Using these relationships, we assessed the models' ability to predict actual moth high altitudinal limits (Fig. 3). As a general pattern models predict moth survival at higher altitudes than the maximum altitude were moth have ever been observed so far (i.e. 3350, 3800 and 3500 m.a.s.l. for *P. operculella*, *S. tangolias*, and *T. solanivora*, respectively). Sharpe and DeMichele's model greatly overestimates this limit for *P. operculella* and *T. solanivora* (predicting survival at altitudes higher than 4000 m.a.s.l.), while the altitudinal limit predicted by Régnière's model is closer to the observed (Fig. 3a and c). While models predict very similar altitudinal limits for *S. tangolias*, they differ more sharply for *T. solanivora*. It is important to note that these altitudinal limits are valid for the Ecuadorian Andes and that moth altitudinal distribution in other places (i.e. Peru or Bolivia) may differ due to different climatic conditions in such places or to local adaptations of insects. No correlation was found between moth predicted survival and observed abundance (Appendix S4). Neither a logarithmic nor a polynomial model fit significantly to the data (R^2 values ranged between 0.21 and 0.39).

Discussion

Comparing various models of insect survival

Accurately predicting the level of success of an invasive insect species in a particular territory necessitates a good description of its climatic niche (Baker et al. 2000, Jarvis and Baker 2001, Sinclair et al. 2003, Logan et al. 2007). Most studies on temperature-related performance have focused on development rate to develop predictive phenological models for insects (Logan 1988, Bentz et al. 1991, Doerr et al. 2002, Gilbert et al. 2004, Ma and

Bechinski 2008). Fewer studies have modeled the influence of temperature on survival (Perez-Mendoza et al. 2004, Bonato et al. 2007), even though it constitutes a direct measurement of organisms' tolerance and is an essential component of fitness (Gilchrist 1995, Angilletta 2009). Particularly, in places where temperatures approach the lethal extremes, a precise assessment of the physiological limits of the species is important for predicting accurately the risk posed by invasive pests (Régnière et al. submitted). In the specific case of the Ecuadorian Andes, mean temperatures at high altitudes may be frequently close to the lower threshold temperatures for survival, and species' distribution is restricted to altitudes with suitable temperatures (Dangles et al. 2008).

In this study we compared the ability of three different models to predict temperature-related PTM survival. We were particularly interested in assessing the behavior of these models when fitted with a small data set that did not cover the whole possible temperature range. Small data sets are indeed a common caveat for many agricultural pests in the tropics, thereby impeding sound predictions of insect survival at temperature extremes (Keller 2003, Niño 2004, Sporleder et al. 2004, Jaramillo et al. 2009). Our study revealed that overestimation of survival probability at low temperatures, by Sporleder's and Sharpe and DeMichele's model, and in a lesser extent by Regniere's model caused overestimation of the maximum altitude that allows survival. This could mean that the actual upper range distribution of these species may not be limited by low temperatures but by other factors such as biotic interactions (competition and predation) or by the absence of potato cultures at higher altitudes. This suggests future lines of research for these species in order to better assess the actual factors limiting their altitudinal distribution.

Potential applications

Accurate measures of tolerance are crucial as well for predicting the consequences of global changes on pests' fitness and distributions (Deutsch et al. 2008, Jaramillo et al. 2009). Based on simulations of warming tolerance of the Coffee Berry Borer, *Hypothenemus hampei*, Jaramillo et al. (2009) predicted devastating effects of global warming on future coffee production. Survival models are useful for evaluating the risk posed by pest species to farmers' crop and agricultural products (Tang et al. 2008, Wang et al. 2009). Agricultural landscapes in tropical countries are highly threatened by an increasing number of pest species, but studies are scarce and data are difficult to obtain. We hence believe that the value of the

Regnière's model lies in its ability to simulate more accurately PTM survival at low and high temperatures when fitted to very few data.

In agreement with Dangles et al.'s (2008) study, our results confirm that the potato tuber moth *S. tangolias* is relatively resistant to cold temperatures and that its current altitudinal limit at 3800 m.a.s.l. may be related to the distribution of potatoes rather than a physiological impediment of cold temperatures. Indeed model extrapolation from figure 3 predicts that this species may be found up to around 4000 m.a.s.l., while its actual distribution is limited to 3800 m.a.s.l. Thus, we infer that the upward expansion of the agricultural frontier in the Ecuadorian Andes (Gondard and Mazurek 2001) may be accompanied by an expansion of *S. tangolias'* distribution to higher altitudes.

Acknowledgments

This work was part of the research conducted within the project *Innovative Approaches for integrated Pest Management in changing Andes* (C09-031) funded by the McKnight Foundation. This work was part of VCP's doctoral project, financed by grants from the French Embassy in Ecuador and from the *Département Soutien et Formation des communautés scientifiques du Sud* (DSF) of the IRD.

References

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

Angilletta, M. J., P. H. Niewiarowski, and C. A. Navas. 2002. The evolution of thermal physiology in ectotherms. Journal of Thermal Biology **27**:249-268.

Baker, R. H. A., C. E. Sansford, C. H. Jarvis, R. J. C. Cannon, A. MacLeod, and K. F. A. Walters. 2000. The role of climatic mapping in predicting the potential geographical distribution of non-indigenous pests under current and future climates. Agriculture Ecosystems & Environment **82**:57-71.

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

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

Dangles, O., C. Carpio, A. R. Barragan, J. L. Zeddam, and J. F. Silvain. 2008. Temperature as a key driver of ecological sorting among invasive pest species in the tropical Andes. Ecol Appl **18**:1795-1809.

Dangles, O., C. Carpio, M. Villares, F. Yumisaca, B. Liger, F. Rebaudo, and J. F. Silvain. 2010. Community-Based Participatory Research Helps Farmers and Scientists to Manage Invasive Pests in the Ecuadorian Andes. AMBIO. **39**:325-335.

Dangles, O., V. Mesias, V. Crespo-Perez, and J. F. Silvain. 2009. Crop damage increases with pest species diversity: evidence from potato tuber moths in the tropical Andes. J Appl Ecol **46**:1115-1121.

Deutsch, C. A., J. J. Tewksbury, R. B. Huey, K. S. Sheldon, C. K. Ghalambor, D. C. Haak, and P. R. Martin. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. PNAS **105**:6668–6672.

Doerr, M. D., J. F. Brunner, and V. P. Jones. 2002. Temperature-dependent development of *Lacanobia subjuncta* (Lepidoptera : Noctuidae). Environmental Entomology **31**:995-999.

Drost, Y. C., J. C. van Lenteren, and H. J. W. van Roermund. 1998. Life-history parameters of different biotypes of *Bemisia tabaci* (Hemiptera : Aleyrodidae) in relation to temperature and host plant: a selective review. Bulletin of Entomological Research **88**:219-229.

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

Gilchrist, G. W. 1995. Specialists and Generalists in Changing Environments .1. Fitness Landscapes of Thermal Sensitivity. American Naturalist **146**:252-270.

Gondard, P., and H. Mazurek. 2001. 30 años de reforma agraria y colonización en el Ecuador (1964–1994): dinámicas espaciales. Estudio de Geografía.

Huey, R. B., and J. G. Kingsolver. 1989. Evolution of thermal sensitivity of ectotherm performance. Trends in Ecology & Evolution **4**:131-135.

Janisch, E. 1932. The influence of temperature on the life-history of insects. Transactions of the Entomological Society of London **80**:137-168.

Jaramillo, J., A. Chabi-Olaye, C. Kamonjo, A. Jaramillo, F. E. Vega, H. M. Poehling, and C. Borgemeister. 2009. Thermal tolerance of the coffee berry borer *Hypothenemus hampei*: Predictions of climate change impact on a tropical insect pest. Plos One **4**.

Jarvis, C. H., and R. H. A. Baker. 2001. Risk assessment for nonindigenous pests: 1. Mapping the outputs of phenology models to assess the likelihood of establishment. Diversity and Distributions **7**:223-235.

Keller, S. 2003. Integrated Pest Management of the Potato Tuber Moth in Cropping Systems of Different Agroecological Zones. Margraf Publishers, Germany.

Logan, J. A. 1988. Toward an Expert System for Development of Pest Simulation-Models. Environmental Entomology **17**:359-376.

Logan, J. A., and J. Powell. 2001. Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). American Entomologist **47**:160-172.

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

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

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

Nyssen, J., J. Poesen, and J. Deckers. 2009. Land degradation and soil and water conservation in tropical highlands. Soil Till Res **103**:197-202.

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

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

Price, P. W. 1997. Insect ecology. Wiley, New York.

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

Régnière, J., and B. Bentz. 2007. Modeling cold tolerance in the mountain pine beetle, Dendroctonus ponderosae. Journal of Insect Physiology **53**:559-572.

Régnière, J., J. Powell, B. Bentz, and V. Nealis. submitted. Temperature Responses of Insects: Design of Experiments, Data Analysis and Modeling. Ecological Applications.

Régnière, J., and A. Sharov. 1998. Phenology of Lymantria dispar (Lepidoptera : Lymantriidae), male flight and the effect of moth dispersal in heterogeneous landscapes. International Journal of Biometeorology **41**:161-168.

Rondon, S. I. 2010. The Potato Tuberworm: A Literature Review of Its Biology, Ecology, and Control. American Journal of Potato Research **87**:149-166.

Roux, O. 1993. Population ecology of potato tuber moth *Phthorimaea operculella* (Zeller) (Lepidoptera:Gelechiidae) and design of an integrated pest management program in Tunisia. SWISS FEDERAL INSTITUTE OF TECHNOLOGY, Zurich.

Schoolfield, R. M., P. J. H. Sharpe, and C. E. Magnuson. 1981. Non-Linear Regression of Biological Temperature-Dependent Rate Models Based on Absolute Reaction-Rate Theory. Journal of Theoretical Biology **88**:719-731.

Schwarz, G. 1978. Estimating dimension of a model. Annals of Statistics **6**:461-464.

Sharpe, P. J. H., and D. W. DeMichele. 1977. Reaction-kinetics of poikilotherm development. Journal of Theoretical Biology **64**:649-670.

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

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

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

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

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

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

Wang, X. G., M. W. Johnson, K. M. Daane, and H. Nadel. 2009. High summer temperatures affect the survival and reproduction of olive fruit fly (Diptera: Tephritidae). Environmental Entomology **38**:1496-1504.

Tables

Table 1. Sources of survival (S) data, temperatures at which the experiments were realized, and immature stage for which data was available for the three species of potato tuber moth.

Species	Data source	Temp.	Stage
P. operculella			
	Sporleder et al. (2004)	10.6	Eggs, Larvae
		10.7	Pupae
		16.0	Pupae
		16.1	Eggs, Larvae
		20.3	Eggs, Larvae, Pupae
		23.0	Eggs, Larvae, Pupae
		24.0	Eggs, Larvae
		25.0	Larvae, Pupae
		26.1	Eggs
		26.2	Pupae
		26.3	Larvae
		26.5	Pupae
		26.7	Eggs
		28.0	Larvae
		30.0	Larvae
		30.2	Pupae
		31.0	Eggs
S. tangolias			
	Dangles et al. (2008)	10.0	Eggs, Larvae, Pupae
		15.0	Eggs, Larvae, Pupae
		20.0	Eggs, Larvae, Pupae
	Palacios et al. (1998)	12.6	Eggs, Larvae, Pupae
		13.0	Eggs, Larvae, Pupae
		17.4	Eggs, Larvae, Pupae
T. solanivora			
	Dangles et al. (2008)	10.0	Eggs, Larvae
		15.0	Eggs, Larvae, Pupae
		20.0	Eggs, Larvae, Pupae
	Torres et al. (1997)	20.0	Eggs, Larvae, Pupae
		25.0	Eggs, Larvae, Pupae

Table 2. Goodness of fit and BIC of the 3 models fitted to survival data of eggs, larvae and pupae of the three species of PTM. *k*, number of parameters fitted; *n*, number of data used to fit the model; LL, log likelihood; *RSS*, residual sum of square.

	EGGS			**LARVAE**			**PUPAE**		
	Sharpe	Sporleder	Régnière	Sharpe	Sporleder	Régnière	Sharpe	Sporleder	Régnière
P. operculella									
-LL	35.904	37.152	35.944	60.864	40.489	45.365	30.249	32.593	26.771
k	6	3	3	6	3	3	5	3	3
n	9	9	9	9	9	9	8	8	8
BIC	84.99	80.90	**78.48**	134.91	**87.57**	97.32	70.90	71.42	**59.78**
S. tangolias									
RSS	0.047	0.062	0.053	0.019	0.020	0.029	0.003	0.003	0.009
k	5	3	3	5	3	2	5	3	2
n	6	6	6	6	6	6	6	6	6
BIC	-20.09	-22.02	**-22.96**	-25.72	**-28.92**	-28.44	-37.04	**-40.71**	-35.64
T. solanivora									
-LL	19.516	19.096	25.403	30.623	30.789	36.072	11.433	12.732	14.307
k	4	3	3	4	3	3	3	2	3
n	5	5	5	5	5	5	4	4	4
BIC	45.47	**43.02**	55.63	67.68	**66.41**	76.97	**27.03**	28.24	32.77

Figure captions

Fig. 1. Survival probability in relation to temperature of eggs, larvae and pupae of *P. operculella* (a, b, c), *S. tangolias* (d, e, f), and *T. solanivora* (g, h, i). Bullets represent observed survival and lines predicted survival by the three models.

Fig. 2. Predicted survival of *P. operculella* (a, b, c), *S. tangolias* (d, e, f) and *T. solanivora* (g, h, i) by the three models in the Ecuadorian Andes.

Fig. 3. Predicted survival rates (bullets) of *P. operculella*, *S. tangolias*, and *T. solanivora* by the three models in 50 sites located along an altitudinal gradient in the Ecuadorian Andes. Predicted survival of *P. operculella*, *S. tangolias*, and *T. solanivora* were adjusted to linear, cubic, and second order polynomial models respectively. Adjusted models are represented by lines. The gray area symbolizes altitudes above the agricultural frontier, where no crop is cultivated (Gondard and Mazurek 2001), and arrows represent maximum altitudes were moth have been recorded during field monitoring in Ecuador.

Figures

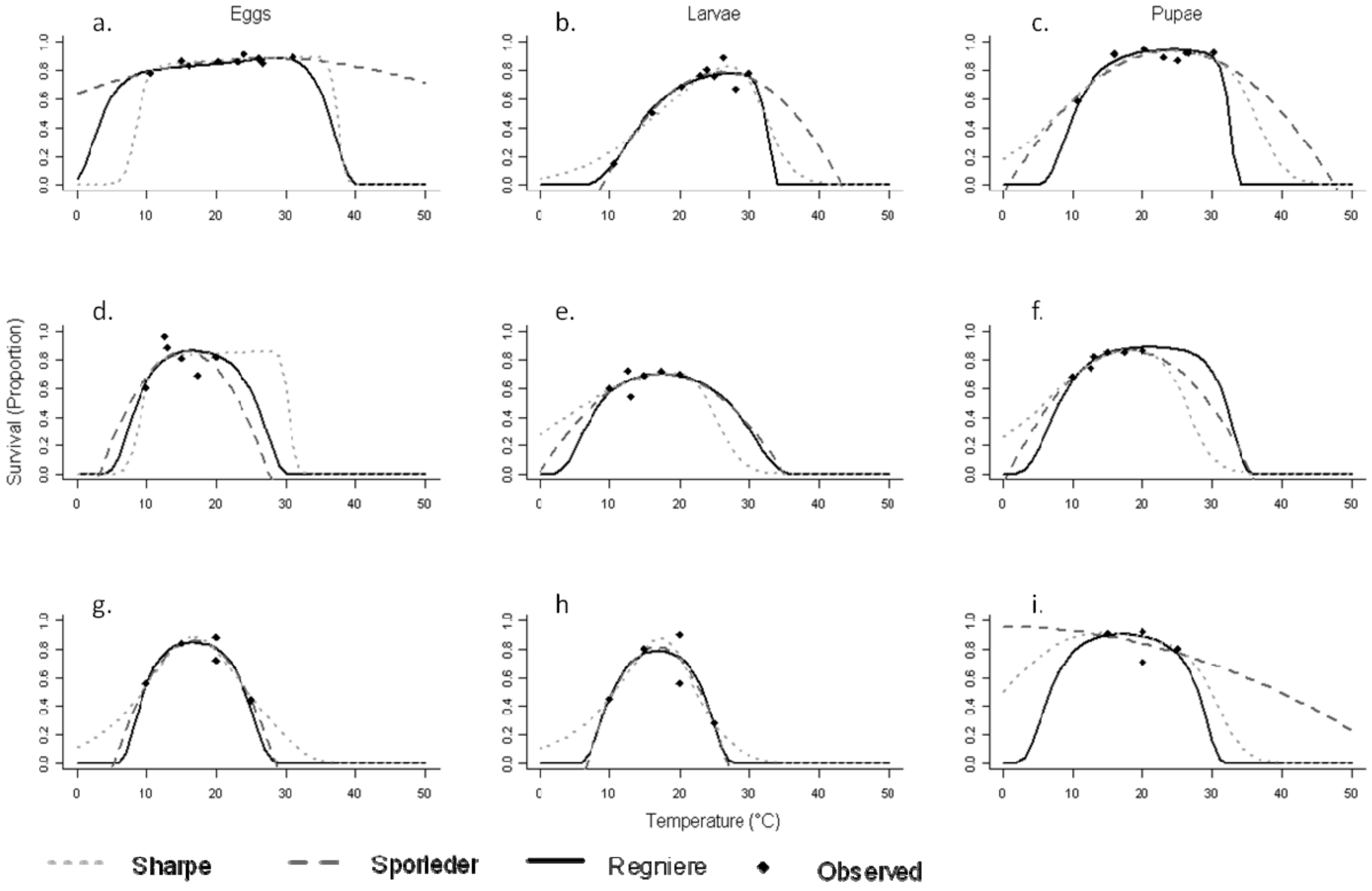


Fig. 1.

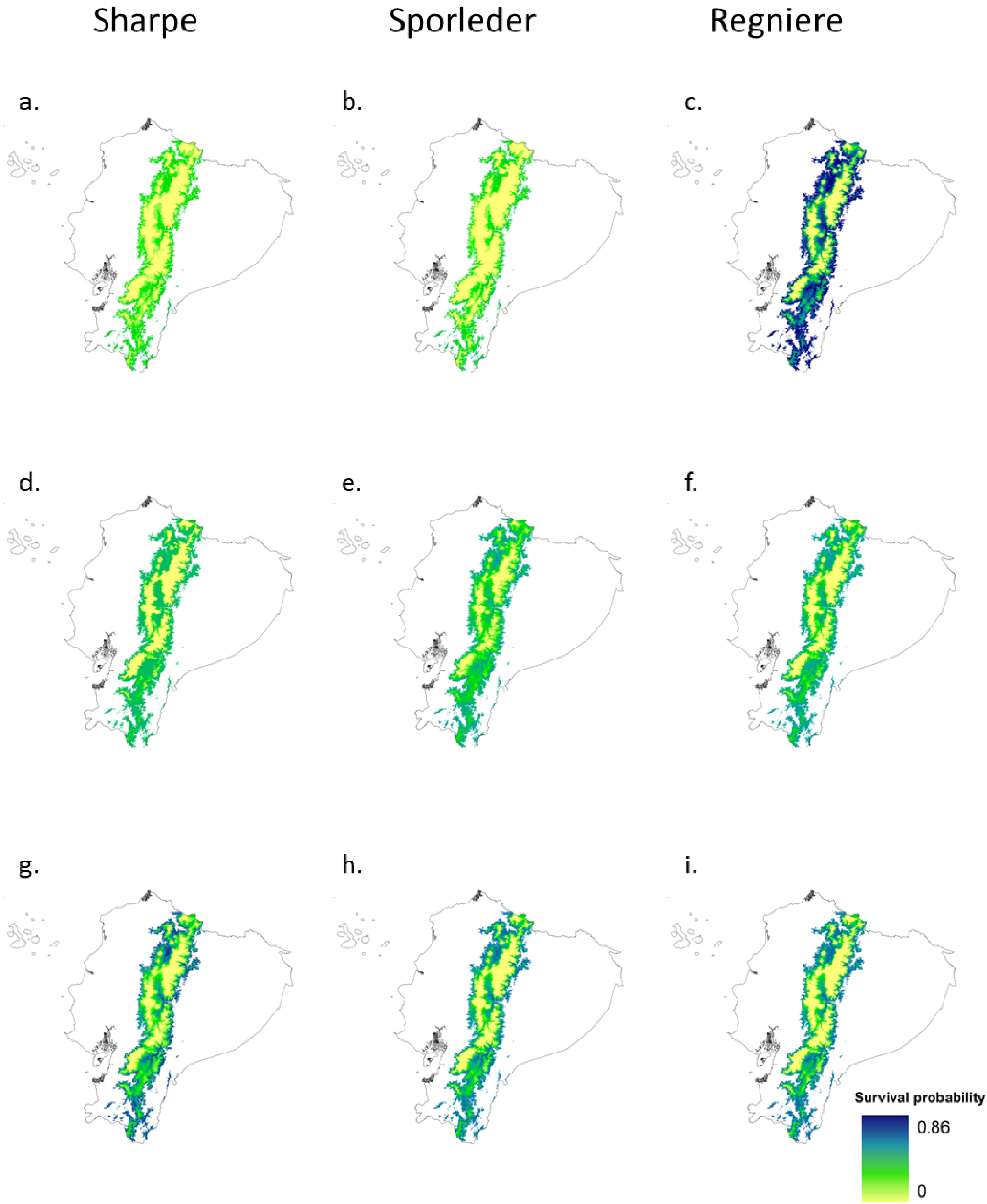

Sharpe
Sporleder
Regniere
a.
b.
c.
d.
e.
f.
g.
h.
i.
Survival probability
0.86
0

Fig. 2.

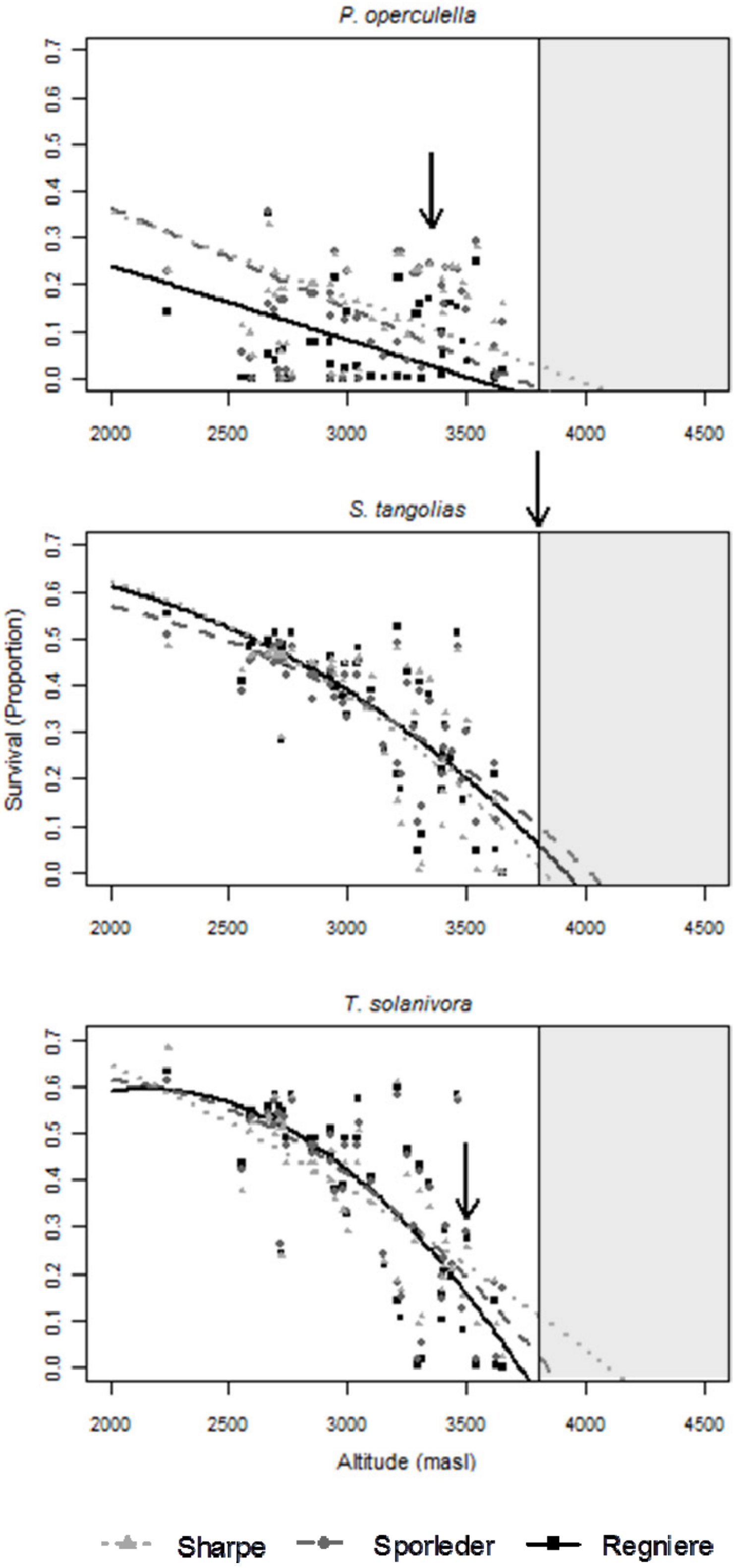

P. operculella
S. tangolias
T. solanivora
Survival (Proportion)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
2000
2500
3000
3500
4000
4500
Altitude (masl)
Sharpe
Sporleder
Regniere

Fig. 3.

APPENDICES CHAPTER 3

APPENDIX S3 – Modeling potato tuber moth temperature-related development time

Data on development of immature stages (eggs, larva, and pupa) of the three species of PTM were acquired from published data of laboratory experiments performed in the Andean region (Table 1). From these sources, only data acquired under constant temperatures (± 2°C) were considered. In all studies, relative humidity ranged from 60 to 90%.

Table 1. Sources of development (D) data and temperatures at which the experiments were realized for the three immature stages of the three species of potato tuber moth.

	Data source	Temp.	Egg
P. operculella	Dangles et al. (2008)	10.0	Eggs, larvae
		15.0	Eggs, larvae, pupae
		20.0	Eggs, larvae, pupae
	Gamboa and Notz (1990)	15.0	Eggs
		20.0	Eggs
		25.0	Eggs
		30.0	Eggs
	Sporleder et al. (2004)	10.6	Eggs, larvae
		10.7	Pupae
		15.0	Eggs
		16.0	Pupae
		16.1	Eggs, larvae
		20.3	Eggs, larvae, pupae
		23.0	Eggs, larvae, pupae
		24.0	Eggs, larvae
		25.0	Larvae, pupae
		26.1	Eggs
		26.2	Pupae
		26.3	Larvae
		26.5	Pupae
		26.7	Eggs
		28.0	Larvae
		30.0	Larvae
		30.2	Pupae
		31.0	Eggs
S. tangolias	Dangles et al. (2008)	10.0	Eggs, larvae, pupae
		15.0	Eggs, larvae, pupae
		20.0	Eggs, larvae, pupae
	Palacios et al. (1998)	12.6	Eggs, larvae, pupae
		13.0	Eggs, larvae, pupae
		17.4	Eggs, larvae, pupae
T. solanivora	Dangles et al. (2008)	10.0	Eggs, larvae
		15.0	Eggs, larvae, pupae
		20.0	Eggs, larvae, pupae
	Notz (1995)	10.0	Eggs, larvae, pupae
		15.0	Eggs, larvae, pupae
		20.0	Eggs, larvae, pupae
		25.0	Eggs, larvae, pupae
		30.0	Eggs
	Torres et al. (1997)	15.0	Eggs, larvae, pupae
		20.0	Eggs, larvae, pupae
		25.0	Eggs, larvae, pupae

Analysis

We analyzed developmental time directly, rather than rate for three reasons: 1) time is what we actually measure in the experiments; 2) an error in developmental time does not coincide with the same error in its inverse, developmental rate at all temperatures (Bentz et al. 1991); 3) when development at low temperatures is important or when development occurs over a long time span (which may be the case for high altitude sites in the Andes), fitting developmental functions to time data should produce a more accurate representation of phenology (Bentz et al. 1991). Developmental time and rate are related by:

$$\tau(T,A)=\frac{1}{r(T,A)} \tag{1}$$

where $\tau(T,A)$ is the simulated mean time for stage completion at temperature T, and A is the vector of parameters of the development rate function $r(T,A)$.

We modeled development of each immature phase with the Sharpe and DeMichele (1977) function (as modified by Schoolfield et al. 1981).

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

where T is temperature in °Kelvin (°C+273.15), R=1.987, and d, e, f, g, h, and i parameters to be estimated. This model has already been employed successfully to model *P. operculella*'s development rate (Sporleder et al. 2004).

We estimated parameter values using maximum likelihood with Microsoft Excel's Solver ®. We therefore assumed that the mean development time is near-normally distributed (central limit theorem). Thus, the probability of observing mean time $\bar{t}_j$ (with standard error s_j) in treatment j at temperature T_j, given the predicted time τ_j is:

$$p\left(\bar{t}_j \middle| \tau_j\right)=\frac{1}{\sqrt{2\pi s_j}}e^{-\frac{1}{2}\left[\left(\bar{t}_j-\tau_j\right)/s_j\right]^2} \tag{3}$$

and the likelihood to maximize is:

$$LL = \sum \ln\left[p\left(\bar{t}_j \middle| \tau_j\right)\right] \tag{4}$$

In the case of *S. tangolias* for which we did not dispose of values of standard error for half of the data, we were forced to adjust the parameters through the method of least sum of squares. However, to avoid unrealistic over-fitting due to the limited amount of data points, we adjusted only parameter ρ_{25} and kept the others fixed to the values obtained for the other species and stages.

Modelled developmental times

Potato tuber moth development data of the three stages of the three species were described adequately by the Sharpe and DeMichele equation (Fig. 1). The relationship between observed and predicted developmental time data is shown in figure 2 and estimated parameter values and log-likelihood values are shown in table 2.

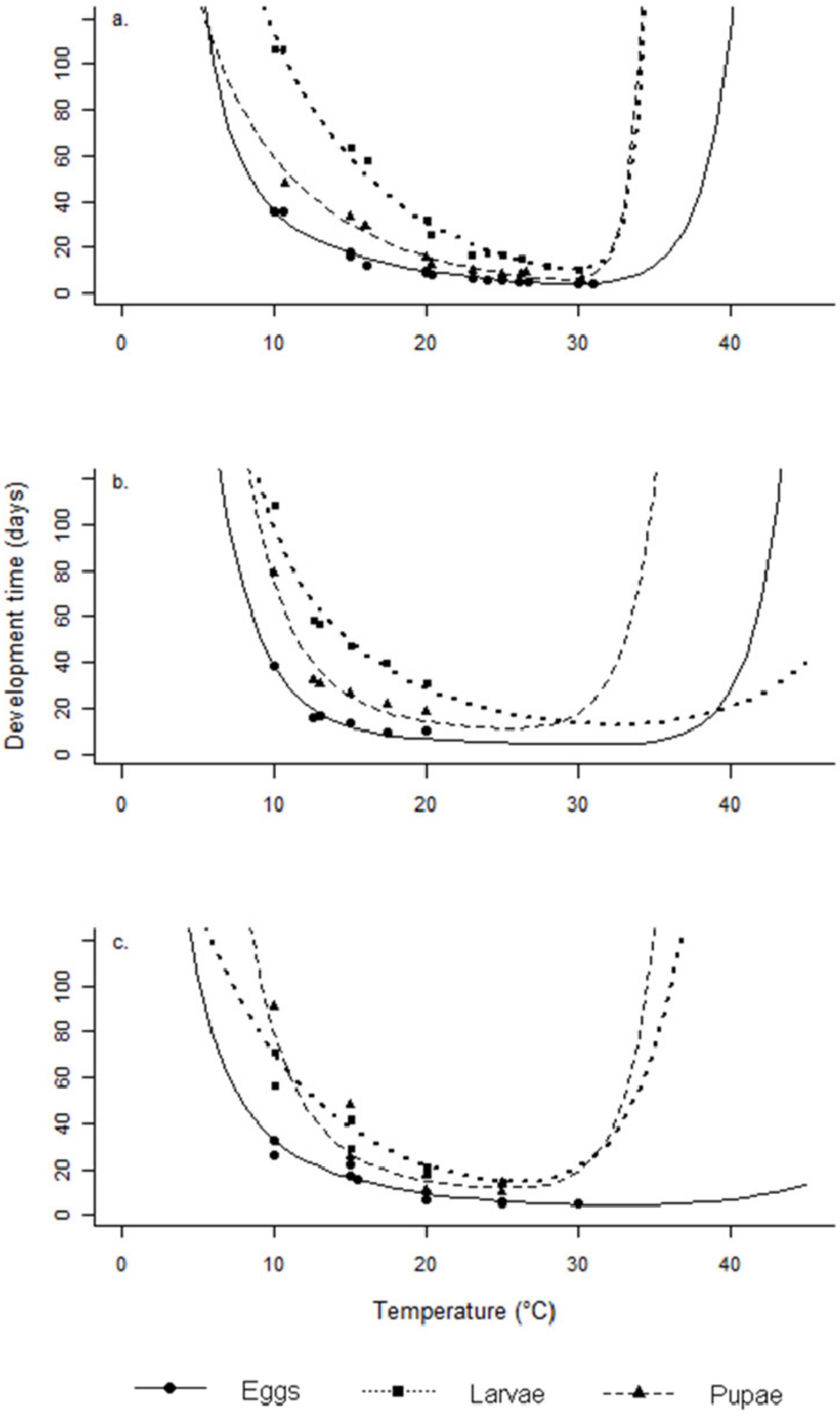


Fig. 1. Observed (bullets) and predicted (lines) developmental times of eggs, larvae and pupae of a) *P. operculella*, b) *S. tangolias*, and c) *T. solanivora*.

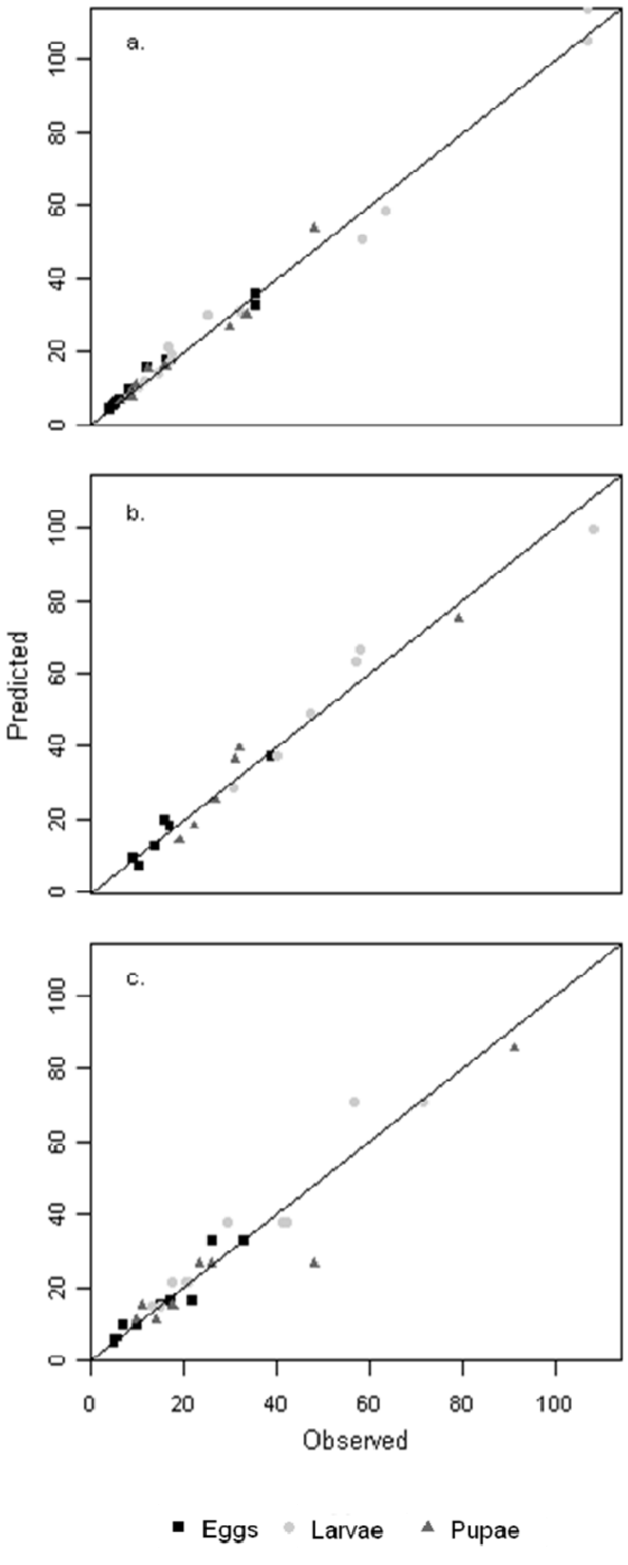


Fig. 2. Observed versus predicted developmental time values for the three immature stages of a) *P. operculella*, b) *S. tangolias*, and c) *T. solanivora*.

Table 2. Parameter estimates and log-likelihood of the Sharpe and DeMichel model adjusted to published laboratory data.

	P. operculella			*S. tangolias*			*T. solanivora*		
	Eggs	Larvae	Pupae	Eggs	Larvae	Pupae	Eggs	Larvae	Pupae
d	0.183	0.060	0.118	0.207	0.059	0.103	0.179	0.114	0.093
e	1.90x10^{4}	2.10x10^{4}	2.10x10^{4}	5.75x10^{3}	1.66x10^{4}	5.75x10^{3}	1.66x10^{4}	1.80x10^{4}	5.75x10^{3}
f	-7.46x10^{4}	-7.46x10^{4}	-7.46x10^{4}	-5.22x10^{4}	-4.97x10^{4}	-5.22x10^{4}	-4.97x10^{4}	-5.00x10^{3}	-5.22x10^{4}
g	279.04	245.15	274.00*	287.03	278.96	287.03	278.96	264.50	287.03
h	1.12x10^{5}	2.21x10^{5}	2.21x10^{5}	1.00x10^{5}	4.95x10^{4}	1.00x10^{5}	4.95x10^{4}	7.67x10^{4}	1.00x10^{5}
i	305.36	305.00	304.19	309.00	307.82	309.00	307.82	300.80	309.00
-LL	242.75	81.57	71.26	0.95*	0.94*	0.95*	839.37	1254.73	1218.49

* R^{2}

References

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

Dangles, O., C. Carpio, A. R. Barragan, J. L. Zeddam, and J. F. Silvain. 2008. Temperature as a key driver of ecological sorting among invasive pest species in the tropical Andes. Ecol Appl **18**:1795-1809.

Gamboa, M., and A. Notz. 1990. Biología de *Phthorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae) en papa (*Solanum tuberosum*). Revsita de la Facultad de Agronomia (Maracay) **16**:245-257.

Notz, A. 1995. Influencia de la temperatura sobre la biologia de *Tecia solanivora* (Povolny) (Lepidoptera: Gelechiidae) criadas en tuberculos de papa *Solanum tuberosum* L. Boletín de Entomología Venezolana **11**:49-54.

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

Schoolfield, R. M., P. J. H. Sharpe, and C. E. Magnuson. 1981. Non-Linear Regression of Biological Temperature-Dependent Rate Models Based on Absolute Reaction-Rate Theory. Journal of Theoretical Biology **88**:719-731.

Sharpe, P. J. H., and D. W. DeMichele. 1977. Reaction-kinetics of poikilotherm development. Journal of Theoretical Biology **64**:649-670.

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

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

APPENDIX S4 – Relationships between survival and abundance and influence of altitude on abundance and on survival.

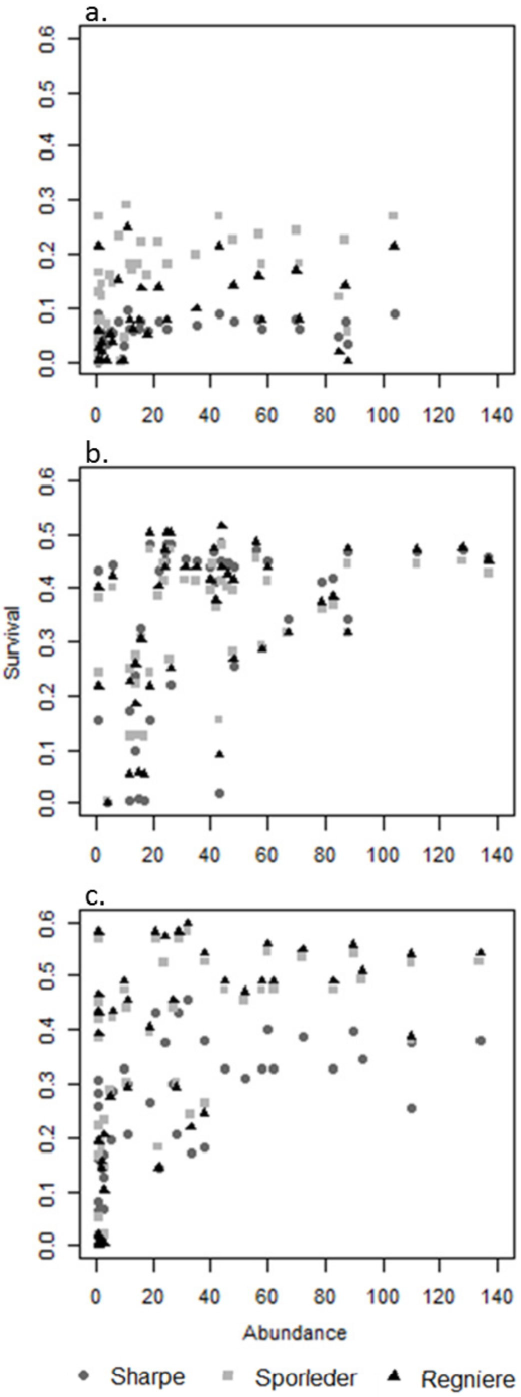


Fig. 1. Predicted survival by the three models in relation to observed abundance at 50 sites in the Ecuadorian Andes of a) *P. operculella*, b) *S. tangolias*, and c) *T. solanivora*.

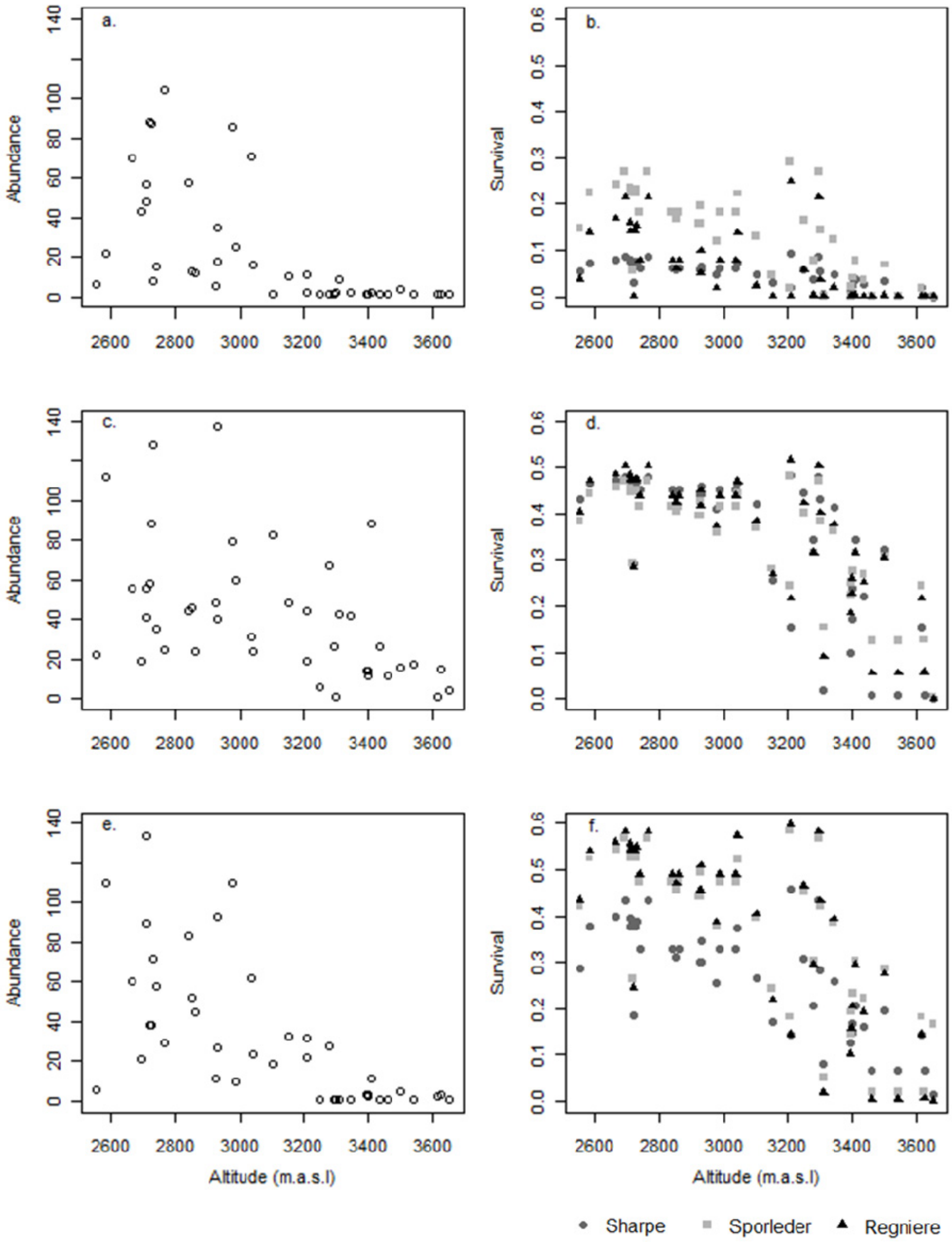


Fig. 2. Relationship between observed abundance at 50 sites in the Ecuadorian Andes and altitude (a, c, e) and between predicted survival by the three models and altitude (b, d, f).

CHAPTER 4

Pest risk mapping in highly heterogeneous regions: The case of Potato Tuber Moth in the Tropical Andes

Verónica Crespo-Pérez[1,2,3], Jacques Régnière[4], Isabelle Chuine[3], François Rebaudo[1], Olivier Dangles[1,2]

[1] IRD, UR 072, Diversité, Ecologie et Evolution des Insectes Tropicaux, Laboratoire Evolution, Génomes et Spéciation, UPR 9034, CNRS, 91198 Gif-sur- Yvette Cedex, France and Université Paris-Sud 11, 91405 Orsay Cedex, France

[2] Laboratorio de Entomología, Facultad de Ciencias Exactas y Naturales, Pontificia Universidad Católica del Ecuador, 12 de Octubre, 1076 y Roca, Quito, Ecuador

[3] Centre d'Ecologie Fonctionnelle et Evolutive, CNRS, 1919 route de Mende, 34293 Montpellier cedex 5, France

[4] Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, PO Box 10380 Stn. Ste Foy, Quebec, QC, Canada G1V 4C7

[5] E-mail: verocrespoperez@yahoo.com

Corresponding author: V. Crespo-Pérez, verocrespoperez@yahoo.com

Abstract

Insect dynamics are highly affected by the temperature of their environment. Variability in temperatures, both diurnal and seasonal or along altitudinal and latitudinal gradients imposes additional pressures for insect life. Accounting for the effect of temperature and its fluctuation on pest population dynamics is important for the construction of realistic simulation models of their dynamics. Such models may be employed in the construction of Pest Risk Maps that describe the probability of pests invading or establishing across a region or landscape. In this study we develop an individual based model that works with simulated climatic conditions under the software BioSim, to predict temperature-related popupation dynamics of three species of Potato Tuber Moth in the North Andean Region. We also assess the impact of future climatic change scenarios on the distribution of the three species. Our results highlight the influence of climatic variability on pest physiology and performance. Our future projections support the theory that range shifts towards higher altitudes will probably be more important in the tropics than latitudinal shifts. We comment on the challenges associated with pest risk mapping in highly heterogeneous landscapes like the Tropical Andes and suggest lines of further research and work to improve the reliability of our prediction.

Key words:

Climate change, climatic variability, heterogeneous landscapes, individual based model, Pest risk mapping, *Phthorimaea operculella*, Potato tuber moth, *Symmetrischema tangolias, Tecia solanivora*

Introduction

Temperature is a key environmental factor determining ectotherm fitness (Angilletta 2009). Insect development, survival, reproduction and locomotion are highly affected by the temperature of their environment (Gould et al. 2005, Dangles et al. 2008, Opit et al. 2010), causing insect distribution to be strongly tied to differences in temperature across regions (Messenger 1959, Régnière et al. 2009). In nature, organisms are subject to seasonal and diurnal fluctuations in temperature. These variations impose pressures to insect physiology and performance and may modify their dynamics at small and large scales of time (Worner 1992, Gilchrist 1995, Angilletta 2009).

The importance of temperature fluctuation on ectotherm life has been interesting biologists for a long time. Seasonal fluctuation is partly responsible for seasonal rhythms in populations and causes adaptations such as dormancy and diapause, especially in the most seasonally variable environments (Denlinger 1986). Daily fluctuations have a “within generation” effect meaning that they affect organisms of the same generation. Most studies about the influence of daily variability on insects’ dynamics have focused on temperature-dependent developmental rate (Kaufmann 1932, cited in Worner 1992). There is little consensus on the actual effects of such variability with some studies finding that development is retarded (Elligsen 1969, cited in Behrens et al. 1983), others that it is accelerated (Hagstrum and Hagstrum 1970, Hagstrum and Leach 1973, Behrens et al. 1983, Davis et al. 2006), and yet others that variability has no apparent effect on development (Morris and Fulton 1970, Humpesch 1982). The effects of temperature variability on dynamics are a consequence of the non-linearity of the temperature-rate relationship of insect performance (Gilbert et al. 2004). In the case of development this phenomenon is known as the rate summation or Kauffman effect (Worner 1992, Bryant et al. 1999) and predicts acceleration of development at low fluctuating temperatures and retardation where temperatures approach into the high temperature threshold when compared to development at constant temperatures (Worner 1992).

All landscapes do not present the same levels of diurnal and seasonal variation. Gradients such as those of altitude and of latitude cause differences in the ranges of temperatures. Levels of seasonal variation are strongly tied to latitudinal gradients. For instance, annual temperature ranges are higher in temperate zones than in the unseasonal tropical ones (Piper and Stewart 1996, Clarke and Gaston 2006, Angilletta 2009). Patterns in daily temperature ranges are less clear, seem to have received less attention in the literature, and can be confounded in some places by local peculiarities or daily fluctuations in solar radiation (Linacre 1982). Temperature measurements performed by our team in the Tropical Andes have revealed that the degree of daily variation is influenced by altitude (Dangles and Carpio, unpubl. data). Low altitude sites have more constant diel temperatures, while at high altitudes temperature during the day may substantially increase (even to more than 30 °C) due to high solar radiation and usually drops close or below 0 °C at night. Based on this evidence, we argue that the theoretical framework of seasonal (among generations) and daily (within generations) thermal variations, initially proposed by Gilchrist (1995, fig. 3) would be a useful one to study temperature variability along altitudinal and latitudinal ranges in the Tropical Andes. Our proposed framework (Fig. 1) predicts increased seasonality from lower to higher latitudes (from 0 to 20°S), and increased diel variations from lower to higher altitudes (from 0 to over 6000 m.a.s.l.).

The abovementioned variations will certainly cause differences in population dynamics of species living along latitudinal and latitudinal gradients. Deeper knowledge about these differences allows more accurate predictions of species performance and distribution along varying environments. The ability to predict species phenology and distribution allows the construction of pest risk maps, which constitute essential tools widely used in pest management to improve the efficiency and timing of pest control programs (Jarvis and Baker 2001a, b, Satake et al. 2006, Logan et al. 2007, Régnière et al. 2009, Venette et al. 2010). These types of maps may be also used in conjunction with predictions of future climate in order to forecast future risks associated with the pests. Human induced climate changes are projected to be intensified in the future (IPCC 2007). Risk related to invasive pests will most likely also change, both in intensity and distribution. Predicting these changes will therefore improve the adaptation of farmers to climatic changes and ameliorate their capacity to prevent and control future attacks by pest species.

In highly heterogeneous regions, such as the Tropical Andes, realism and reliability of phenology and distribution models and of pest risk maps strongly depend on their ability to reproduce the influence of such variability on the dynamics of the target species. In this contribution we describe the development of a physiologically based climate suitability model for evaluating present and future risk of invasion of the Potato Tuber Moth (PTM, Lepidoptera, Gelechiidae) in the Tropical Andes. 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). Accurately predicting current and future range related to these species is imperative for improving the livelihoods and food security of hundreds of thousands of farmers of the region.

Materials and Methods

Study region

The following study was realized in 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 (Plate 1). We concentrated in areas exceeding 1000 m.a.s.l. because potato is only cultivated above such altitudes. The total area considered comprised 2 033 000 km^2. One of the most prominent features of the study region is its marked spatial heterogeneity, mainly related to changes in elevation (Young and Lipton 2006, Young 2009). The region also lacks a marked seasonality in temperature, especially close to 0° of latitude. As latitude increases, however, temperature seasonality becomes more apparent (Dangles et al. unpubl. data). The Tropical Andes do present temporal variability in environmental conditions mainly related to variations in precipitation. Nevertheless, precipitation patterns in the Tropical Andes are complex and difficult to predict since they are influenced by several factors such as 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).

Data bases

The approach developed in this contribution required detailed data on topographic variation of the region, which was obtained with Digital Elevation Models (DEM's) and on historical and future weather variation. DEM information was used to interpolate weather station data to the whole region.

Digital elevation models

We used digital elevation models (DEM's) of the North 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).

Weather/Climate

Historical weather data were obtained from several sources: 1) 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/gsod/); 2) Global Historical Climatology Network (GHCN) data from the National Oceanic and Atmospheric Administration (NOAA); 3) 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 was obtained from the International Centre for Tropical Agriculture's 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 CO_2 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.

Potato tuber moth model

We constructed an individual based model of PTM dynamics to mimic moth responses to temperature in the North Andean Region. This model simulated development, survival and fecundity rate models for the three species of PTM based on their stage-specific response functions to temperature. We used published temperature-response data of laboratory experiments performed in the Andean region (Torres et al. 1997, Palacios et al. 1998, Sporleder et al. 2004, Dangles et al. 2008) and unpublished data from laboratory experiments performed by our team at Entomology Laboratory of the Pontifical Catholic University of Ecuador to construct temperature-based models of insects' dynamics (see Chapters 1 and 2 of this dissertation).

PTM development rate was modeled with the Sharpe and DeMichele (1977) equation as modified by Schoolfield et al. (1981):

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

where T is temperature in °Kelvin (°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 larvae, larvae to pupae or pupae to adult). Variability in developmental rates 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.

Temperature related survival probability for each stage of each species was calculated with equation 2:

$$P(survival)=\left(\frac{e^{a+bT+cT^2}}{1+e^{a+bT+cT^2}}\right)^{D(T)} \tag{2}$$

where a, b, and c are estimated parameters. Individual survival during each time step was simulated by drawing a uniformly-distributed random number and removing the individual if this number was larger than the survival probability during that time step. See chapter 3 of this dissertation for a detailed description of the development and survival models.

Number of eggs laid by each female accumulating from the onset of the oviposition period to time t was modeled with equation 3:

$$O_t = F_0\left(1-e^{-\kappa(T,B)(t-t_0)}\right) \tag{3}$$

where F_0 represents temperature related fecundity:

$$F_0 = j + kAbs\left|T - T_o\right|^x \tag{4}$$

where j, k, T_o and x are estimated parameters. κ from equation 3 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 and DeMichele's model modified by Schoolfield *et al.* (1981). Since sex ratio of PTM species is close to one (Herrera 1998, Makee and Saour 2001) half of the pupae that transformed into adults were considered as oviposing females. Adult longevity in relation to temperature was also modeled with the modified Sharpe and DeMichele (1977) model. See chapter 2 of this dissertation for a detailed description of the oviposition rate model.

We used eqation 5 to calculate population growth rate at each time step:

$$N_{E_{t+1}} = N_{E_t} S_{E_t}(T) + O_{t+1} \tag{5}$$

with N_E the number of eggs at time t and S_E survival probability as a function of temperature (T) at time t, and O number eggs laid by females at time t+1. Model time step was four hours with temperatures interpolated by half sine curves between successive daily minimum and maximum values.

Assessing the influence of temperature variation on population dynamics

In order to understand the importance of the degree of seasonal and daily temperature fluctuations on PTM dynamics we ran the model for one year at nine sites located across an altitudinal and latitudinal gradient. We chose sites where temperature variations resembled those of Figure 1. We used the BioSIM system to generate daily weather data for each site and simulate our insects' dynamics (see *Weather Interpolation* section below).

PTM risk mapping

We implemented the PTM models into the BioSIM system (Régnière 1996) in order to obtain maps of target events such as PTM population survival, mean number of generations and population growth rate in the North 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 have been found to begin at 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 North Andean Region. The BioSIM modeling process is explained in more detail below.

Weather 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 CIAT's future temperature data and current temperature from the WorldClim data set (Hijmans et al. 2005). This difference was then applied to the weather station data.

Given the influence of daily variability on insect performance (Worner 1992, Liu et al. 2002, Meats and Kelly 2008) BioSIM interpolates linearly between monthly mean temperatures to produce daily maximum/minimum temperature values for simulations (Régnière and Bolstad 1994, Régnière and St-Amant 2007, Régnière et al. 2008). Time step in our model was set to four hours and temperatures were interpolated by half sine curves between successive daily minimum and maximum values to simulate variation along the day.

Model runs and output interpolation

We ran the models for 10 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=). We ran 5 replications for each location and obtained values of mean number of generations per year, mean population growth rate and mean survival for each replication at each location. 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 performance in the North 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 http://www.innomip.ird.fr 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 and 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 for 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 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 the threshold according to the smallest non-zero predicted survival probability value for each species. 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 observed adult abundance through time with predicted adult abundance after five years of simulations. Since we were interested in patterns rather than actual numbers and the differences between observed and predicted numbers were too large, we were forced to transform the data (log-transformation).

Results

Influence of temperature variation on population dynamics

Levels of diurnal and seasonal temperature variability affected the three species of PTM in different ways (Fig. 2). *P. operculella*'s population growth was enhanced with smaller diurnal and seasonal fluctuations, with fastest growth at the warmer low altitude and low latitude site (Fig. 2a). In general, increase in latitude (i.e. increase in seasonal variability) was detrimental for this species' growth, with the population becoming extinct after a little more than six months at the high altitude and high latitude sites. Both *S. tangolias* and *T. solanivora* populations were unable to persist at low altitude sites, presumably due to their lower tolerance to higher temperatures (Fig. 2b and 2c, respectively). Increase in diurnal fluctuations with altitude slowed down these two species' dynamics. *T. solanivora*'s population went rapidly extinct at sites with high seasonal variation (Fig. 2c).

Predicted current distribution

Predictions of PTM dynamics in the Tropical Andes (above 1000 m.a.s.l.) showed that *P. operculella* had in general a higher probability of surviving than the other two species (Fig. 3a). *T. solanivora* showed the lowest overall survival (Fig. 3c) and according to our model none of the species were able to survive in the highest parts of Bolivia (the Altiplano) although the presence of *P. operculella* and *S. tangolias* has been recorded by our team at several monitoring sites of this landscape (Fig. 3a and b and see http://www.innomip.ird.fr/). The other two target events (number of generations and population growth rate) presented similar patterns and are shown in Appendix A3. In general, the three species performed better at lower than higher altitudes. A zoom to the Ecuadorian Andes showed that the models were able to predict survival of the three species in the sites of observed presence (Fig.4). Results for number of generations and population growth rate produced similar patterns than those for survival probability in the Ecuadorian Andes (results not shown).

According to the AUC our predictions for *P. operculella* were no better than random. (AUC = 0.44, $P = 0.87$). This is probably caused by the fact that the model fails to predict presence in the majority of monitoring sites of Peru and Bolivia and predicts high survival at lower altitudes where we dispose of no data on the species presence or absence. These two phenomena are probably the cause of the low hit rate and the high false alarm rate observed in the ROC curve (Fig. 5a). However, according to the one-tailed binomial test, with a threshold of 0.01, the probability of our model predicting the localities of observed moth presence was significant ($P < 0.05$). Our model performed better for the other two species (Fig. 4b and c). Predictions for *S. tangolias* were fair with an AUC of 0.61 ($P < 0.05$) and those for *T. solanivora* were good (AUC = 0.86, $P < 0.001$). ROC curves for these two species can be observed in Fig. 5b and c. One-tailed binomial test, with thresholds of 0.2 for both species, also showed that our model predicted these two species' survival in observed localities significantly better than random ($P < 0.001$).

Comparing the observed and predicted number of adults at several monitoring sites in the study region showed that in many of the sites where moth presence is constantly observed the model predicts a persistent adult population (Fig 6). We did not find clear temporal patterns in observed and predicted adult abundance. The model predicted population extinction for *P. operculella* and *S. tangolias* in the Bolivia site, even though adult moth presence is constantly detected there (Fig. 6a and b, respectively). The same occurs in the high altitude site of Central Peru for *P. operculella*. In the case of *T. solanivora*, whose southern distribution limit is Southern Ecuador, the model did not predict population persistence in Peru or Bolivia (Fig. 6c).

Predicted future distribution

The future temperature scenarios we used for our projections show that in most parts of the region temperature will tend to increase (Appendix A4). However, in few parts of the Eastern Ecuadorian cordillera and the Colombian Andes temperature is projected to decrease, especially in 2020 with scenario B2. Nevertheless, the level of cooling will not approach more than 1 °C. By 2050 temperature of most of the region will increase by 1 to 3 °C, with most intensive warming in some parts of Peru and Bolivia. According to our PTM phenology model these changes in temperature will change the risk related to PTM distribution (see Fig. 7 for predictions of survival, and Appendix A5 and A6 for number of generations and population growth rate). Our results show that responses will differ among species and between climate change scenarios. In general, we found risk to be higher in scenario A2 as compared to B2 (although differences in 2020 seem very subtle). Also we found that risk tended to increase with time as evidenced by a general increase in survival probability, number of generations per year and population growth rate between 2020 and 2050.

In particular, we found that *P. operculella* and *S. tangolias*'s dynamics will be enhanced, especially in Peru and Bolivia where these species survival probability, number of generations and population growth rate will increase (Fig. 7a and b). According to our model *T. solanivora* will present less risk for potato cultures than the other two species. Future conditions will be favorable for this species mostly in Peru and a few parts of Bolivia (note that currently *T. solanivora* is absent from these two countries). In Ecuador and most parts of Colombia conditions will cause risk related to *T. solanivora* to either remain unchanged or decrease in a small degree.

Cooling will apparently produce different responses among the three species. In Southern Colombia lower temperatures will be detrimental for *P. operculella*'s populations, whereas *T. solanivora*'s and *S. tangolias* dynamics will be enhanced by cooling in some zones. For instance, see these two species' patterns of survival (Fig. 7b and c) and number of generations (Appendix A5, Fig. 2 and 3) in the North Eastern Colombian Andes (Fig. 7c).

Influence of altitude and latitude on actual and future distribution

The three species' current distributions differ with respect to altitude and latitude (Fig. 8). Our results show that currently *P. operculella* is better adapted to lower altitudes whereas the other two seem to perform better at higher altitudes. Increase in latitude seems to be detrimental for the three species as well, with their number of generations, their population growth and their survival probability being lower at the higher latitudes (Fig. 8a, b and c, respectively).

Future climate changes will produce different responses in the three species. Our model suggests an expansion of *P. operculella* towards higher altitudes, as evidenced by the increase in number of generations, population growth rate and survival probability of this species towards higher altitudes in the future (Fig. 8a, b, and c, respectively). Patterns for *S. tangolias* and *T. solanivora* suggest that these two species will contract their distribution ranges. This will be mainly caused by decreased performance at lower altitudes - see for example the decrease in *T. solanivora*'s population growth rate at low altitudes from current conditions to 2050 (Fig. 8b). According to our results *T. solanivora*'s performance will not be greatly enhanced at higher altitudes. On the contrary, future conditions may allow *S. tangolias* to expand its range to higher altitude by increasing its survival probability (Fig. 8c). Also, at low latitude zones population growth rate of this species presents a slight increase towards higher altitudes in the future (Fig. 8b).

Patterns of change with latitude are less evident, especially for *S. tangolias* and *T. solanivora*. At lower latitudes future conditions seem to improve for *P. operculella*. For instance, notice that low altitude populations able to produce eight generations per year are currently projected to be restricted to a narrow range of latitudes (from 0 to 9°). By 2050 conditions will allow populations to produce that same number of generations from 10° to -12° of latitude (Fig. 8a). Survival rate of low altitude populations shows similar trend (Fig. 8c).

Discussion

The approach presented in this study is a first attempt to build present and future pest risk maps of Potato Tuber Moth invasion at the level of the Tropical Andean region. The use of a phenology model allowed us to simulate moth phenology across the region and to assess their probabilities of survival, number of generations and population growth rate under the climatic regimes of the highly variable Tropical Andes. In our study we were interested in two types of temperature variability that may be experienced by PTM along the altitudinal and latitudinal gradients of the Tropical Andes: daily variability whose range is thought to increase with altitude, and seasonal variability, whose range increases with increasing latitude (see Introduction). Studies on temperature variability normally use experiments to determine the different effects of fluctuating versus constant temperatures on insects' performance (Elliott et al. 1988, Joshi 1996, Davis et al. 2006, Meats and Kelly 2008). In our case we simulated PTM dynamics in sites with different levels of seasonal and daily variation with a phenology model calibrated with data obtained at constant temperatures. Output of this model revealed differences in the effects of levels of variation among the three species' dynamics. These results may help understanding the present observed distributions of the species. For instance, *P. operculella*, the most widely spread of the three species across tropical and subtropical countries (Rondon 2010), seemed to be the most tolerant and the most successful, especially in low altitude sites with low daily variation. The other two species, whose distribution is restricted to mountainous regions, were not able to survive in the low altitude sites.

Modeling species distribution at large scales in highly heterogeneous environments is a challenging task for ecologists. In this contribution we managed to simulate *T. solanivora*'s actual distribution successfully, and the model seemed to perform better for the three species in the Ecuadorian part of their distribution. In the case of *P. operculella* and *S. tangolias* we encountered some difficulties when predicting their presence in high parts of Peru and in the Bolivian Altiplano. This may be caused by several factors. First, it may be due to the difficulty of accounting for the actual heterogeneity of the region and to simulate realistic temperature conditions. We simulated temperature by interpolating data from weather stations across the region. In the Andes weather stations are not very abundant. This, added to the high heterogeneity of the region, may reduce the accuracy of weather interpolation. In fact, comparing simulated and observed weather at two sites in Peru and one in Bolivia showed us that simulations were different from observations, with a sub estimation of temperature ranges by the latter (Appendix A7). As pointed out by Worner (1992), when mean temperatures are close to the minimum threshold for development, larger temperature fluctuations may speed up development and thus favor populations in places with these characteristics. This could possibly explain the observed presence of *P. operculella* and *S. tangolias* at our monitoring sites in Bolivia where the model predicted them absent. The importance of collecting more quality weather data for the Andean Region becomes evident. Also, high heterogeneity allows us to suspect that microclimatic conditions could be influencing pest dynamics at some parts of the region. Smaller scale models with more detailed environmental conditions could thus be more useful and realistic for such cases.

Our model's accuracy may have also been reduced by the human-induced heterogeneity or social heterogeneity of the region. The Tropical Andes have a long history of human occupation. Since the arrival of the first humans to the region in the early Holocene the landscape has been subject to anthropogenic impacts first related to burning, hunting and gathering and later to intensive agricultural activity (Johannessen and Hastorf 1990, Hansen and Rodbell 1995, Sarmiento 2002, Young 2009). These alterations may mask or confound the effects of natural drivers of pest invasion and establishment. As shown by a cellular automata model developed by our team to simulate *T. solanivora*'s propagation into an isolated valley of the Central Ecuadorian Andes, the presence of potato storage structures across the territory allows the establishment of moth in places from which they would normally be absent due to climatic constraints (Crespo-Pérez et al. accepted). In fact, the pest's actual propagation was better explained when the model accounted for the presence of storage structures than when it considered the natural landscape alone. Perhaps including the presence and effect of these structures in the present model would allow us to make more realistic predictions of the moths' actual distribution, although this would be a most challenging task at the level of the whole tropical Andean region.

Another challenge related to invasive species distribution modeling is genetic bottleneck associated with invasion. This phenomenon reduces genetic diversity of invading populations and could cause them to respond differently to environmental characteristic. Studies of genetic structure of *T. solanivora* populations across its native and invaded ranges indeed showed a reduction in genetic diversity in invasive populations (Puillandre et al. 2008). Torres et al. (2011) even found that reduction was more drastic in populations from more recently invaded countries (i.e. populations of Colombia, Ecuador and the Canary Islands). We are not aware of similar studies for the other two species of PTM, but given that the mechanisms of invasion of the three are probably the same (through commercial exchanges of potato) we can expect a similar trend in their genetic diversity. Additionally, populations living at different parts of the region with particular weather conditions may be adapted to such conditions and may thus respond differently than populations from other locations (Gilchrist 1995, Angilletta 2009). Lack of sufficient data forced us to calibrate our models with data from a small number of populations that did not cover the entire distribution range of the species, mainly in the case of *P. operculella* and *S. tangolias.* Extrapolating this information to the entire Tropical Andean Region may have biased our prediction. For instance, *P. operculella* performance models were adjusted to data of populations from Peru (Sporleder et al. 2004) and those of *S. tangolias*' to data from Ecuador and Peru (Palacios et al. 1998, Dangles et al. 2008). Thus, our results may suggest that Bolivian populations of these two species may respond differently to temperature and may be able to overcome temperature conditions of the Bolivian Altiplano. We therefore believe that collecting data from a wider geographic range would also aid to enhance the realism of our predictions.

Future risks related to PTM

Running our model with future climate change projections showed us that risks related to PTM will change in the future. Information about the effects of climate change on arthropods comes mainly from studies at temperate regions, with most reporting positive effects on insect fitness and distribution ranges (Parmesan et al. 1999, Bale et al. 2002, Gomi et al. 2007, Musolin 2007, Kearney et al. 2009). Studies in the tropics are less abundant and establishing generalities about the effects of climate change in these regions is difficult (but see Kearney at al. 2009). Some studies report deleterious effects of climate changes on ectotherm diversity (Deutsch et al. 2008) and on geographic distribution of some groups (Terblanche et al. 2008). Others, on the contrary, predict that climate change may be favorable for some species (Patz and Olson 2006, Jaramillo et al. 2009). Our study confirmed that the effects of climate change will vary depending on the species of PTM and on geographic location; although a general favorable influence was evidenced for *P. operculella* and *S. tangolias*.

Theory on responses of species distributions to climate change predicts that in the tropics upslope shifts of range limits will probably be more important than poleward shifts because of the shallow latitudinal temperature gradient between the Tropics of Cancer and Capricorn (Colwell et al. 2008, Kreyling et al. 2010). Our results for *P. operculella* and *S. tangolias* support this theory since higher altitudes will become favorable for the species dynamics in the future. Future conditions in the lower limits of *S. tangolias* current distribution will become less favorable in the future causing this species range to contract at lower altitudes. In addition, we found a much weaker tendency for a shift towards lower latitudes and only for *P. operculella*. Such predictions constitute important tools that may improve adaptation of farmers to changing pest risks associated with future climate warming. In the Tropical Andes, where human activity, especially land use changes, may intensify the effects of climate warming or cause additional impacts to species distribution, predictions of models should incorporate such anthropogenic activities for construction of more realistic pest risk maps for the future.

Acknowledgements

This work was part of the research conducted within the project *Innovative Approaches for integrated Pest Management in changing Andes* (C09-031) funded by the McKnight Foundation. We are grateful to Rémi St. Amant for his assistance with model programming and weather interpolation. We also thank Carlos Carpio and Mario Hererra for their technical support during moth monitoring in the field, Paula Iturralde for her help with ArcGIS and map formatting and Pablo Menendez for his guidance and insightful suggestions for model validation. This work was part of VCP's doctoral project, financed by grants from the French Embassy in Ecuador and from the *Département Soutien et Formation des communautés scientifiques du Sud* (DSF) of the IRD.

References

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

Bale, J. S., G. J. Masters, I. D. Hodkinson, C. Awmack, T. M. Bezemer, V. K. Brown, J. Butterfield, A. Buse, J. C. Coulson, J. Farrar, J. E. G. Good, R. Harrington, S. Hartley, T. H. Jones, R. L. Lindroth, M. C. Press, I. Symrnioudis, A. D. Watt, and J. B. Whittaker. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Global Change Biology **8**:1-16.

Behrens, W., K. H. Hoffmann, S. Kempa, S. Gassler, and G. Merkelwallner. 1983. Effects of diurnal thermoperiods and quickly oscillating temperatures on the development and reproduction of crickets, *Gryllus-Bimaculatus*. Oecologia **59**:279-287.

Bryant, S. R., J. S. Bale, and C. D. Thomas. 1999. Comparison of development and growth of nettle-feeding larvae of Nymphalidae (Lepidoptera) under constant and alternating temperature regimes. European Journal of Entomology **96**:143-148.

Clarke, A., and K. J. Gaston. 2006. Climate, energy and diversity. Proceedings of the Royal Society B-Biological Sciences **273**:2257-2266.

Colwell, R. K., G. Brehm, C. L. Cardelus, A. C. Gilman, and J. T. Longino. 2008. Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. Science **322**:258-261.

Crespo-Pérez, V., F. Rebaudo, J.-F. Silvain, and O. Dangles. accepted. Modeling invasive species spread in complex landscapes: the case of potato moth in Ecuador. Landscape Ecology.

Dangles, O., C. Carpio, A. R. Barragan, J. L. Zeddam, and J. F. Silvain. 2008. Temperature as a key driver of ecological sorting among invasive pest species in the tropical Andes. Ecol Appl **18**:1795-1809.

Davis, J. A., E. B. Radcliffe, and D. W. Ragsdale. 2006. Effects of high and fluctuating temperatures on *Myzus persicae* (Hemiptera : Aphididae). Environmental Entomology **35**:1461-1468.

Denlinger, D. L. 1986. Dormancy in Tropical Insects. Annual Review of Entomology **31**:239-264.

Deutsch, C. A., J. J. Tewksbury, R. B. Huey, K. S. Sheldon, C. K. Ghalambor, D. C. Haak, and P. R. Martin. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. PNAS **105**:6668–6672.

Ellingsen, I. J. 1969. Effect of constant and varying temperature on development, feeding and survival of *Adalia bipunctata* (Coccinellidae). Norweigian Journal of Entomology **16**:121-125.

Elliott, N. C., R. W. Kieckhefer, and D. D. Walgenbach. 1988. Effects of constant and fluctuating temperatures on developmental rates and demographic statistics for the corn leaf aphid (Homoptera, Aphididae). J Econ Entomol **81**:1383-1389.

Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation **24**:38-49.

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

Gilchrist, G. W. 1995. Specialists and Generalists in Changing Environments .1. Fitness Landscapes of Thermal Sensitivity. American Naturalist **146**:252-270.

Gomi, T., M. Nagasaka, T. Fukuda, and H. Hagihara. 2007. Shifting of the life cycle and life-history traits of the fall webworm in relation to climate change. Entomologia Experimentalis Et Applicata **125**:179-184.

Gould, J., R. Venette, and D. Winograd. 2005. Effect of temperature on development and population parameters of *Copitarsia decolora* (Lepidoptera : Noctuidae). Environmental Entomology **34**:548-556.

Hagstrum, D. W., and W. R. Hagstrum. 1970. A Simple Device for Producing Fluctuating Temperatures, with an Evaluation of the Ecological Significance of Fluctuating Temperatures. Annals of the Entomological Society of America **63**:1385-1389.

Hagstrum, D. W., and C. E. Leach. 1973. Role of Constant and Fluctuating Temperatures in Determining Development Time and Fecundity of Three Species of Stored-Products Coleoptera. Annals of the Entomological Society of America **66**:407-410.

Hansen, B. C. S., and D. T. Rodbell. 1995. A late-glacial/Holocene pollen record from the Eastern Andes of Norther Peru. Quaternary Research **44**:216-227.

Herrera, F. 1998. La polilla guatemalteca de la papa: biología, comportamiento y prácticas de manejo integrado. Corporación Colombiana de Investigación Agropecuaria (CORPOICA), Bogotá, Colombia.

Hijmans, R. J. 2001. Global distribution of the potato crop. American Journal of Potato Research **78**:403-412.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. Int J Climatol **25**:1965-1978.

Humpesch, U. H. 1982. Effect of fluctuating temperature on the duration of embryonic development in two <i>Ecdyonurus</i> spp. and <i>Rhithrogena cf. hybrida</i> (Ephemeroptera) from Austrian streams. Oecologia **55**:285-288.

IPCC. 2007. Summary for Policymakers. Cambridge University Press, Cambridge.

Jaramillo, J., A. Chabi-Olaye, C. Kamonjo, A. Jaramillo, F. E. Vega, H. M. Poehling, and C. Borgemeister. 2009. Thermal tolerance of the coffee berry borer *Hypothenemus hampei*: Predictions of climate change impact on a tropical insect pest. Plos One **4**.

Jarvis, A., H. I. Reuter, A. Nelson, and E. Guevara. 2008. Hole-filled SRTM for the globe Version 4, available from the CGIAR-CSI SRTM 90m Database. (http://srtm.csi.cgiar.org).

Jarvis, C. H., and R. H. A. Baker. 2001a. Risk assessment for nonindigenous pests: 1. Mapping the outputs of phenology models to assess the likelihood of establishment. Diversity and Distributions **7**:223-235.

Jarvis, C. H., and R. H. A. Baker. 2001b. Risk assessment for nonindigenous pests: 2. Accounting for interyear climate variability. Diversity and Distributions **7**:237-248.

Johannessen, S., and C. Hastorf. 1990. A history of fuel management (A.D. 500 to the present) in the Mantaro Valley, Peru. Journal of Ethnobiology **10**:61-90.

Joshi, D. S. 1996. Effect of fluctuating and constant temperatures on development, adult longevity and fecundity in the mosquito Aedes krombeini. Journal of Thermal Biology **21**:151-154.

Kearney, M., W. P. Porter, C. Williams, S. Ritchie, and A. A. Hoffmann. 2009. Integrating biophysical models and evolutionary theory to predict climatic impacts on species' ranges: the dengue mosquito Aedes aegypti in Australia. Functional Ecology **23**:528-538.

Kreyling, J., D. Wana, and C. Beierkuhnlein. 2010. Potential consequences of climate warming for tropical plant species in high mountains of southern Ethiopia. Diversity and Distributions **16**:593-605.

Linacre, E. 1982. The effect of altitude on the daily range of temperature. Journal of Climatology **2**:375-382.

Liu, S. S., F. Z. Chen, and M. P. Zalucki. 2002. Development and survival of the diamondback moth (Lepidoptera : Plutellidae) at constant and alternating temperatures. Environmental Entomology **31**:221-231.

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

Makee, H., and G. Saour. 2001. Factors influencing mating success, mating frequency, and fecundity in *Phthorimaea operculella* (Lepidoptera: Gelechiidae). Environmental Entomology **30**:31-36.

Meats, A., and G. L. Kelly. 2008. Relation of constant, daily fluctuating, and ambient feeding temperature to daily and accumulated consumption of yeast autolysate and sucrose by female Queensland fruit fly. Entomologia Experimentalis Et Applicata **129**:87-95.

Messenger, P. S. 1959. Bioclimatic studies with Insects. Annual Review of Entomology **4**:183-206.

Minitab. 2009. Minitab, Release 15. Minitab, Inc., State College, PA.

Morin, X., C. Augspurger, and I. Chuine. 2007. Process-based modeling of species' distributions: What limits temperate tree species' range boundaries? Ecology **88**:2280-2291.

Morris, R. F., and W. C. Fulton. 1970. Models for the development and survival of *Hyphantria cunea* in relation to temperature and humidity. Memoirs of the Entomological Society of Canada **102**:1-62.

Musolin, D. L. 2007. Insects in a warmer world: ecological, physiological and life-history responses of true bugs (Heteroptera) to climate change. Global Change Biology **13**:1565-1585.

Opit, G. P., J. E. Throne, and M. E. Payton. 2010. Reproductive Parameters of the Parthenogenetic Psocid Lepinotus reticulatus (Psocoptera: Trogiidae) at Constant Temperatures. Environmental Entomology **39**:1004-1011.

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

Parmesan, C., N. Ryrholm, C. Stefanescu, J. K. Hill, C. D. Thomas, H. Descimon, B. Huntley, L. Kaila, J. Kullberg, T. Tammaru, W. J. Tennent, J. A. Thomas, and M. Warren. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature **399**:579-583.

Patz, J. A., and S. H. Olson. 2006. Malaria risk and temperature: Influences from global climate change and local land use practices. Proceedings of the National Academy of Sciences of the United States of America **103**:5635-5636.

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling **190**:231-259.

Piper, S. C., and E. F. Stewart. 1996. A gridded global data set of daily temperature and precipitation for terrestrial biospheric modeling. Global Biogeochemical Cycles **10**:757-782.

Poveda, G., D. M. Alvarez, and O. A. Rueda. 2011. Hydro-climatic variability over the Andes of Colombia associated with ENSO: a review of climatic processes and their impact on one of the Earth's most important biodiversity hotspots. Climate Dynamics **36**:2233-2249.

Puillandre, N., S. Dupas, O. Dangles, J. L. Zeddam, C. Capdevielle-Dulac, K. Barbin, M. Torres-Leguizamon, and J. F. Silvain. 2008. Genetic bottleneck in invasive species: the potato tuber moth adds to the list. Biol Invasions **10**:319-333.

R. 2010. R: A language and environment for statistical computing. Page Development Core Team R Foundation for Statistical Computing, Vienna, Austria.

Régnière, J. 1996. Generalized approach to landscape-wide seasonal forecasting with temperature-driven simulation models. Environmental Entomology **25**:869-881.

Régnière, J., and P. Bolstad. 1994. Statistical Simulation of Daily Air Temperature Patterns Eastern North America to Forecast Seasonal Events in Insect Pest Management. Environmental Entomology **23**:1368-1380.

Régnière, J., B. Cooke, and V. Bergeron. 2008. BioSIM: a computerbased decision support tool for seasonal planning of pest management activities. User’s manual. Canadian Forest Service Information Report LAU-X-134, Quebec.

Régnière, J., V. Nealis, and K. Porter. 2009. Climate suitability and management of the gypsy moth invasion into Canada. Biol Invasions **11**:135-148.

Régnière, J., and R. St-Amant. 2007. Stochastic simulation of daily air temperature and precipitation from monthly normals in North America north of Mexico. International Journal of Biometeorology **51**:415-430.

Rondon, S. I. 2010. The Potato Tuberworm: A Literature Review of Its Biology, Ecology, and Control. American Journal of Potato Research **87**:149-166.

Sarmiento, F. O. 2002. Anthropogenic change in the landscapes of highland Ecuador. Geographical Review **92**:213-234.

Satake, A., T. Ohgushi, S. Urano, and K. Uchimura. 2006. Modeling population dynamics of a tea pest with temperature-dependent development: predicting emergence timing and potential damage. Ecological Research **21**:107-116.

Schoolfield, R. M., P. J. H. Sharpe, and C. E. Magnuson. 1981. Non-Linear Regression of Biological Temperature-Dependent Rate Models Based on Absolute Reaction-Rate Theory. Journal of Theoretical Biology **88**:719-731.

Sharpe, P. J. H., and D. W. DeMichele. 1977. Reaction-kinetics of poikilotherm development. Journal of Theoretical Biology **64**:649-670.

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

Terblanche, J. S., S. Clusella-Trullas, J. A. Deere, and S. L. Chown. 2008. Thermal tolerance in a south-east African population of the tsetse fly Glossina pallidipes (Diptera, Glossinidae): Implications for forecasting climate change impacts. Journal of Insect Physiology **54**:114-127.

Torres-Leguizamon, M., S. Dupas, D. Dardon, Y. Gomez, L. Nino, A. Carnero, A. Padilla, I. Merlin, A. Fossoud, J. L. Zeddam, X. Lery, C. Capdevielle-Dulac, O. Dangles, and J. F. Silvain. 2011. Inferring native range and invasion scenarios with mitochondrial DNA: the case of T. solanivora successive north-south step-wise introductions across Central and South America. Biological Invasions **13**:1505-1519.

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

Venette, R. C., D. J. Kriticos, R. D. Magarey, F. H. Koch, R. H. A. Baker, S. P. Worner, N. N. G. Raboteaux, D. W. McKenney, E. J. Dobesberger, D. Yemshanov, P. J. De Barro, W. D. Hutchison, G. Fowler, T. M. Kalaris, and J. Pedlar. 2010. Pest Risk Maps for Invasive Alien Species: A Roadmap for Improvement. Bioscience **60**:349-362.

Williams, J. J., W. D. Gosling, A. L. Coe, S. J. Brooks, and P. Gulliver. 2011. Four thousand years of environmental change and human activity in the Cochabamba Basin, Bolivia. Quaternary Research **76**:58-68.

Worner, S. P. 1992. Performance of phenological models under variable temperature regimes - Consequences of the Kaufmann or rate summation effect. Environmental Entomology **21**:689-699.

Young, K., and J. Lipton. 2006. Adaptive Governance and Climate Change in the Tropical Highlands of Western South America. Climatic Change **78**:63-102.

Young, K. R. 2009. Andean land use and biodiversity: Humanized ladscapes in a time of change. Annals of the Missouri Botanical Garden **96**:492-507.

Figure captions

Fig. 1. Predicted daily and seasonal temperature variability along an altitudinal and latitudinal gradient in the Tropical Andes.

Fig. 2. Population dynamics of the three species of PTM simulated for one year under the climatic conditions of nine sites along an altitudinal and latitudinal gradient in the North Andean Region. Temperature regimes of the nine sites resemble those for the hypothesized temperatures in figure 1. Mean annual temperature for each site is shown in the upper left corner of each graph.

Fig. 3. Maps showing current survival probability predicted by our phenology model for the three species of PTM in the Northern Andes. Simulations were done only in areas over 1000 m.a.s.l., altitude over which potato is cultivated in the region.

Fig. 4. Maps showing predicted survival probability for the three species in a portion of the Ecuadorian Andes.

Fig. 5. Receiver Operating Characteristic curves showing the relationship between hit rate (true positive) and false alarm rate (false positive) for current distribution predictions for a) *P. operculella*, b) *S. tangolias*, and c) *T. solanivora* in the Northern Andes. Numbers along the curves represent the threshold survival over which the species were considered present for each measurement of accuracy.

Fig. 6. Observed and predicted adult numbers (ln transformed and $\log_{10}$ transformed in the case of observed and predicted numbers respectively) at several sites in Ecuador, Peru and Bolivia where a monitoring program has been established. Numbers of predicted adults correspond to numbers for the fifth year of simulation. a) *P. operculella*, b) *S. tangolias*, and c) *T. solanivora.*

Fig. 7. Predicted future survival probability for the four climate change scenarios for a) *P. operculella*, b) *S. tangolias*, and c) *T. solanivora*, showing the anomalies with respect to current predicted survival.

Fig. 8. Contour plots showing the influence of altitude and latitude on present and future a) survival probability, b) number of generations per year, and c) population growth rate of the three species of PTM.

Figures

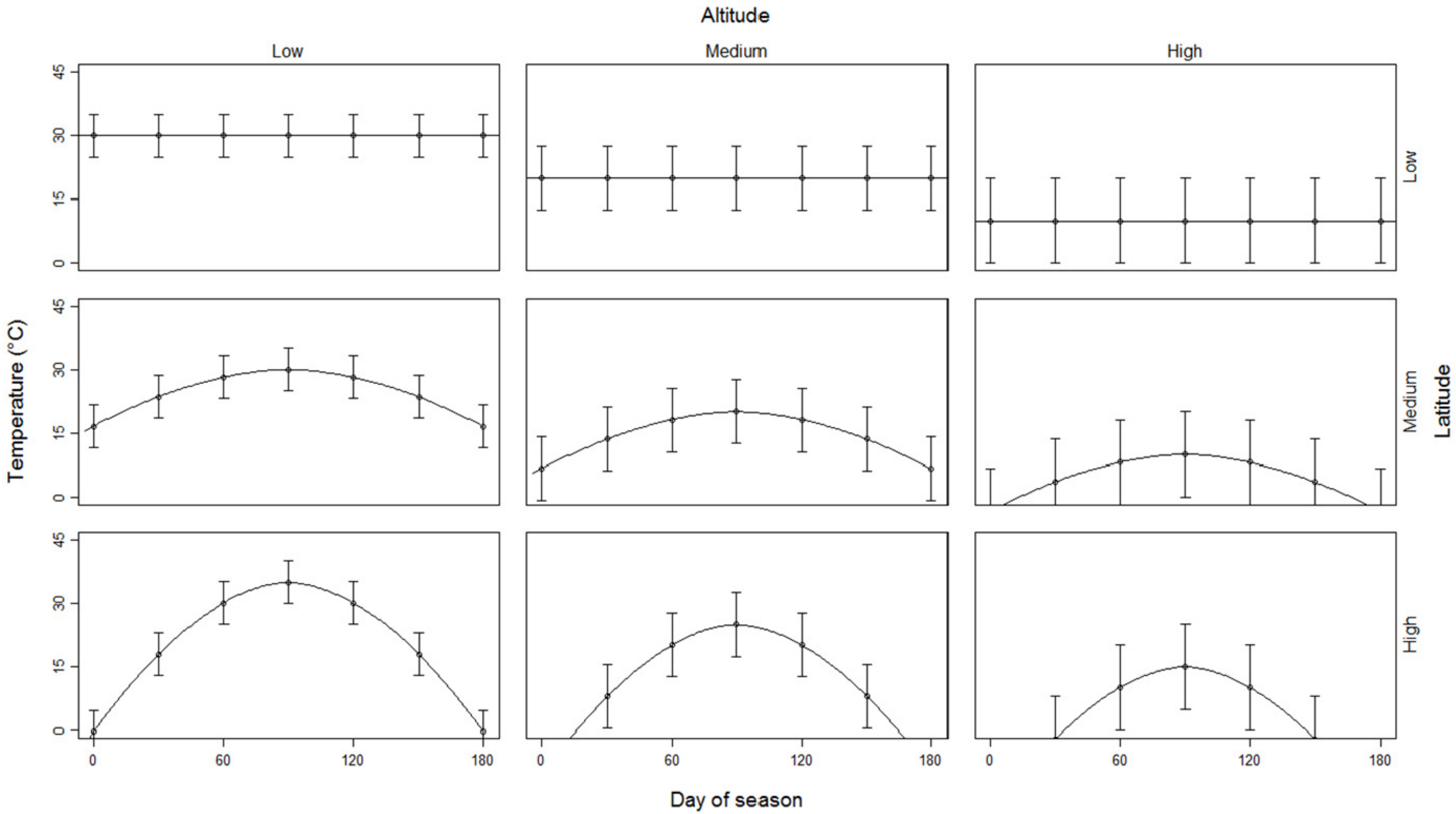


Fig. 1

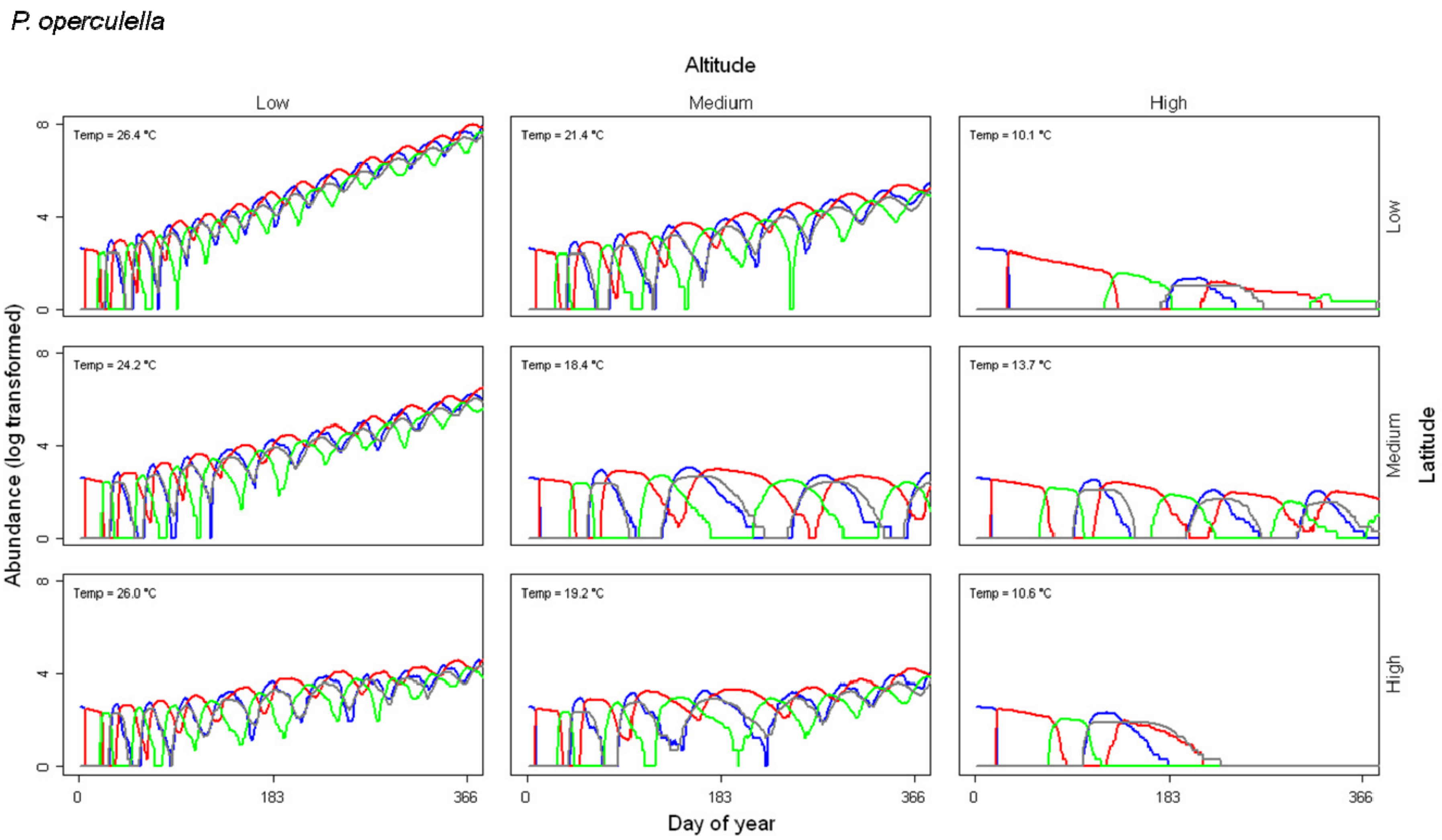

P. operculella
Altitude
Low
Medium
High
Latitude
Low
Medium
High
Abundance (log transformed)
Day of year
0
4
8
0
183
366
Temp = 26.4 °C
Temp = 21.4 °C
Temp = 10.1 °C
Temp = 24.2 °C
Temp = 18.4 °C
Temp = 13.7 °C
Temp = 26.0 °C
Temp = 19.2 °C
Temp = 10.6 °C

Fig. 2a

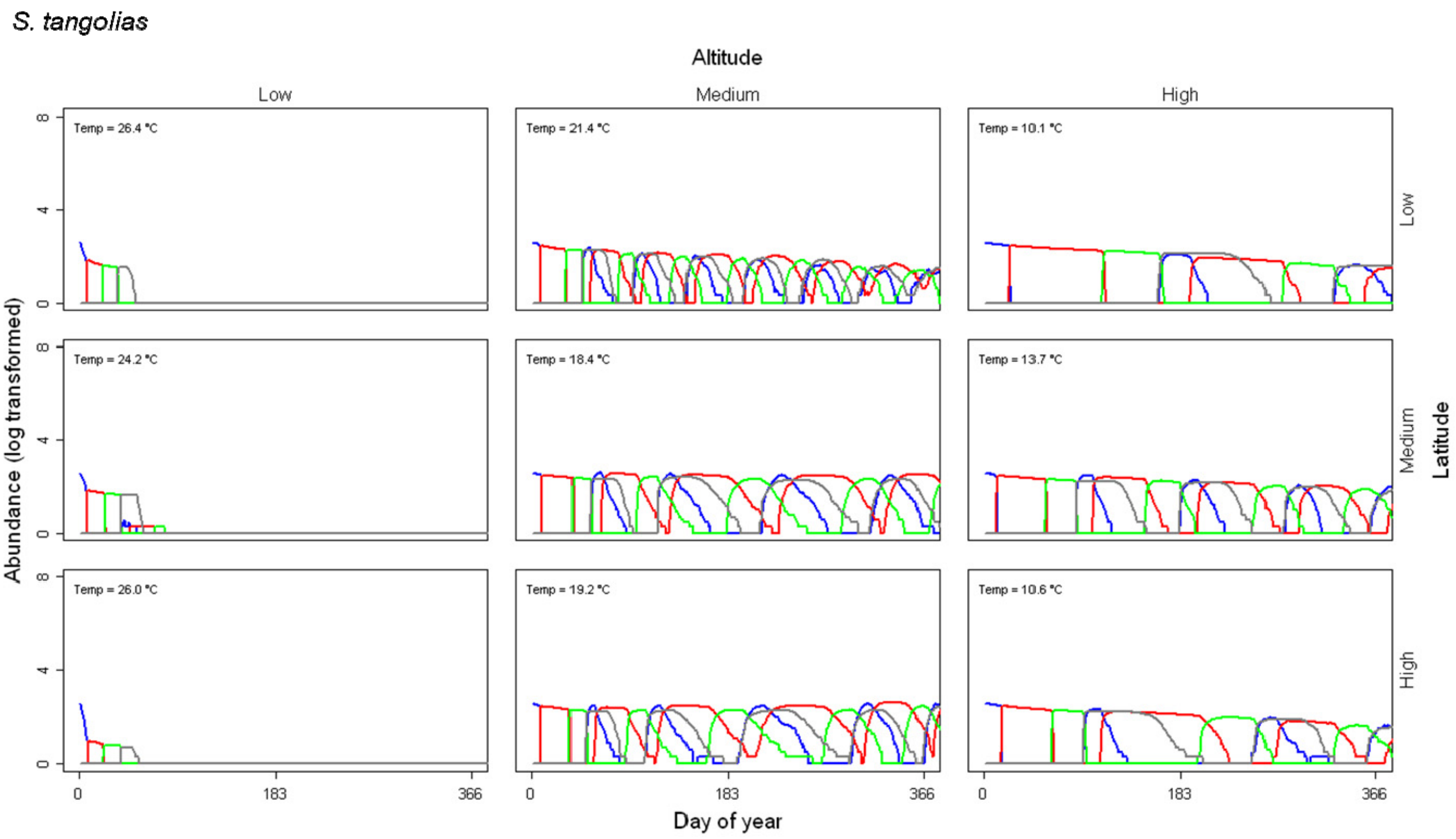

S. tangolias
Altitude
Low
Medium
High
Latitude
Low
Medium
High
Abundance (log transformed)
Day of year
0
4
8
0
183
366
Temp = 26.4 °C
Temp = 21.4 °C
Temp = 10.1 °C
Temp = 24.2 °C
Temp = 18.4 °C
Temp = 13.7 °C
Temp = 26.0 °C
Temp = 19.2 °C
Temp = 10.6 °C

Fig. 2b

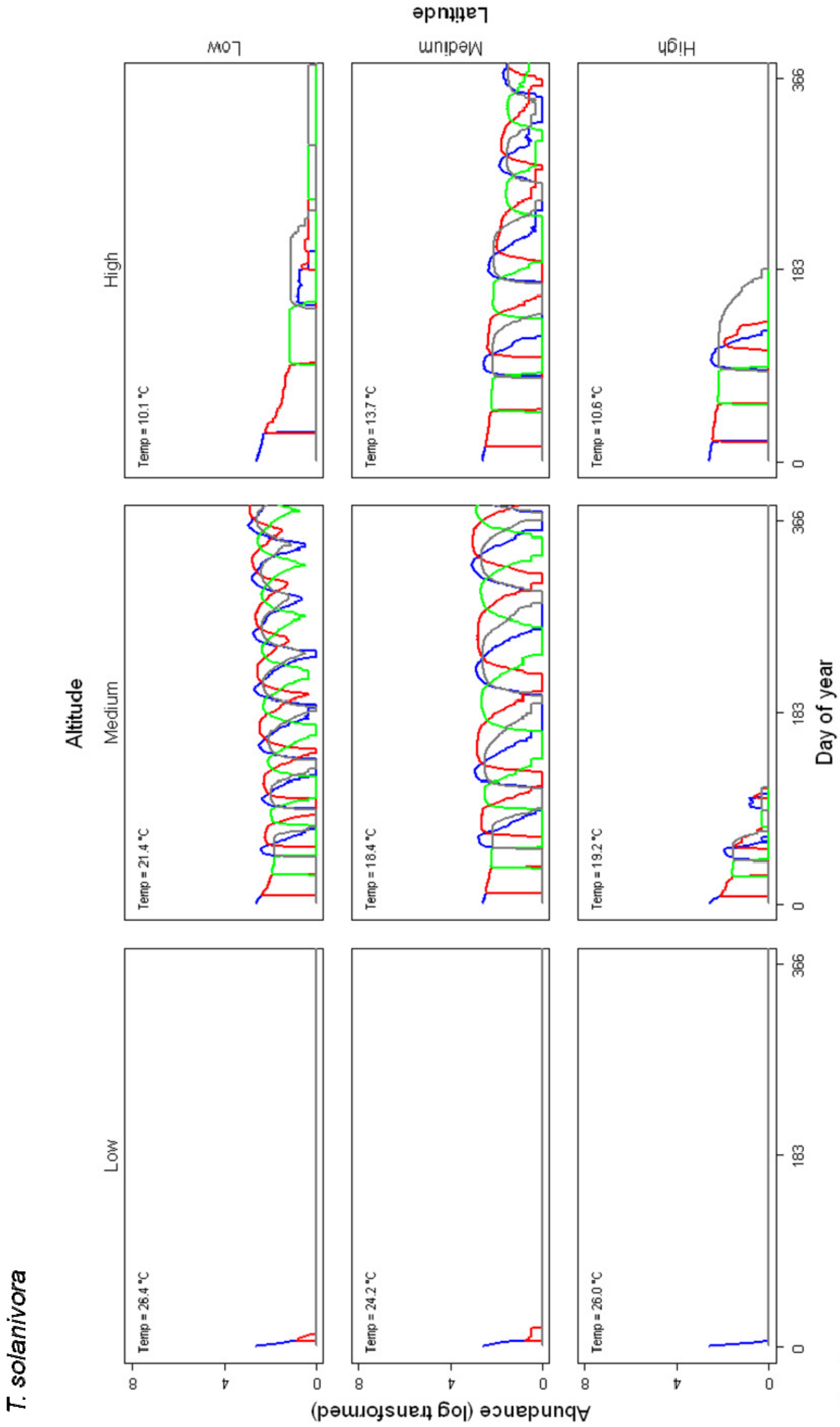

T. solanivora
Altitude
Low
Medium
High
Latitude
Low
Medium
High
Temp = 26.4 °C
Temp = 21.4 °C
Temp = 10.1 °C
Temp = 24.2 °C
Temp = 18.4 °C
Temp = 13.7 °C
Temp = 26.0 °C
Temp = 19.2 °C
Temp = 10.6 °C
Abundance (log transformed)
8
4
0
Day of year
0
183
366

Fig. 2c

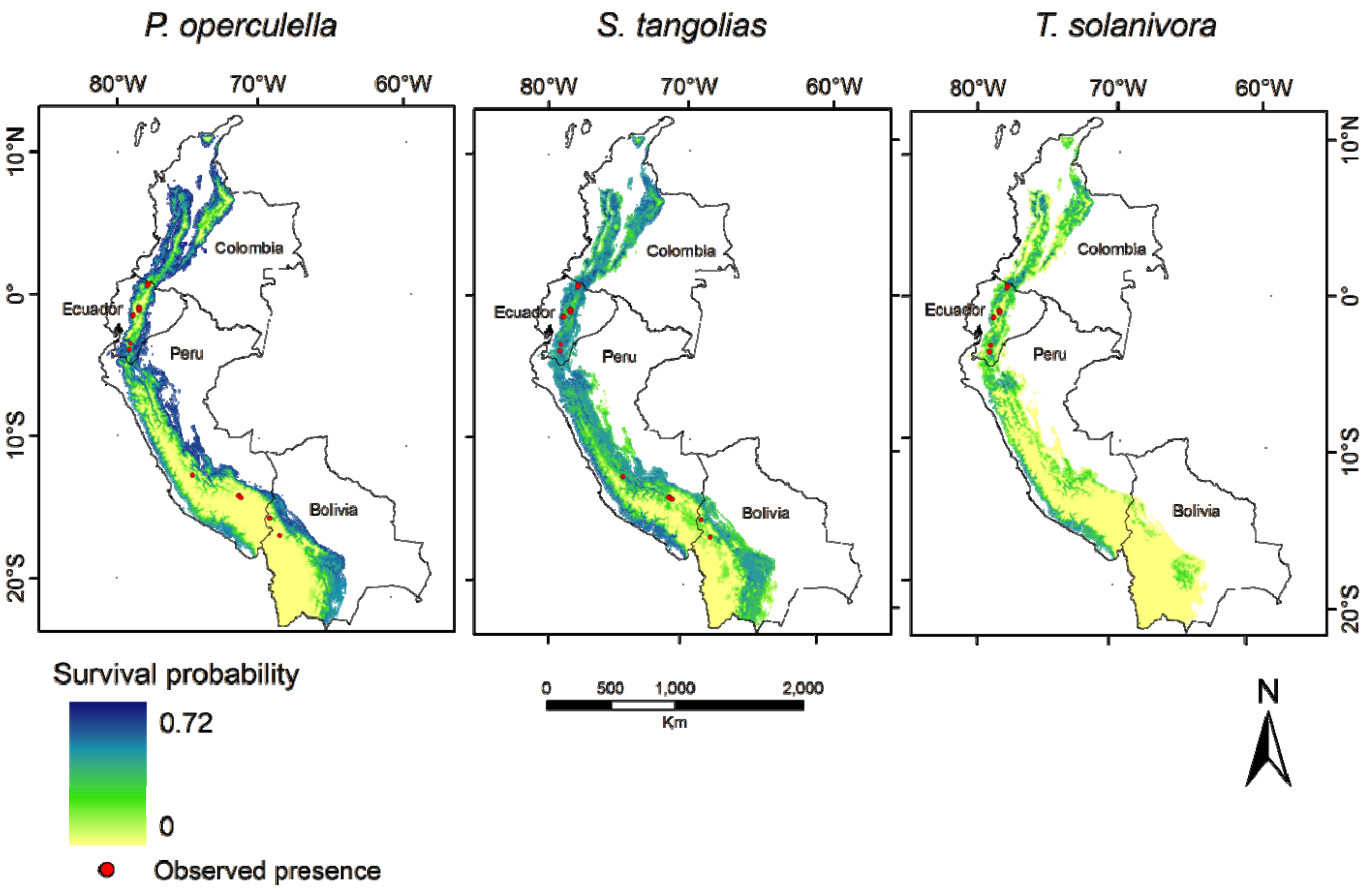

P. operculella
S. tangolias
T. solanivora
80°W
70°W
60°W
10°N
0°
10°S
20°S
Colombia
Ecuador
Peru
Bolivia
Survival probability
0.72
0
Observed presence
0
500
1,000
2,000
Km
N

Fig. 3

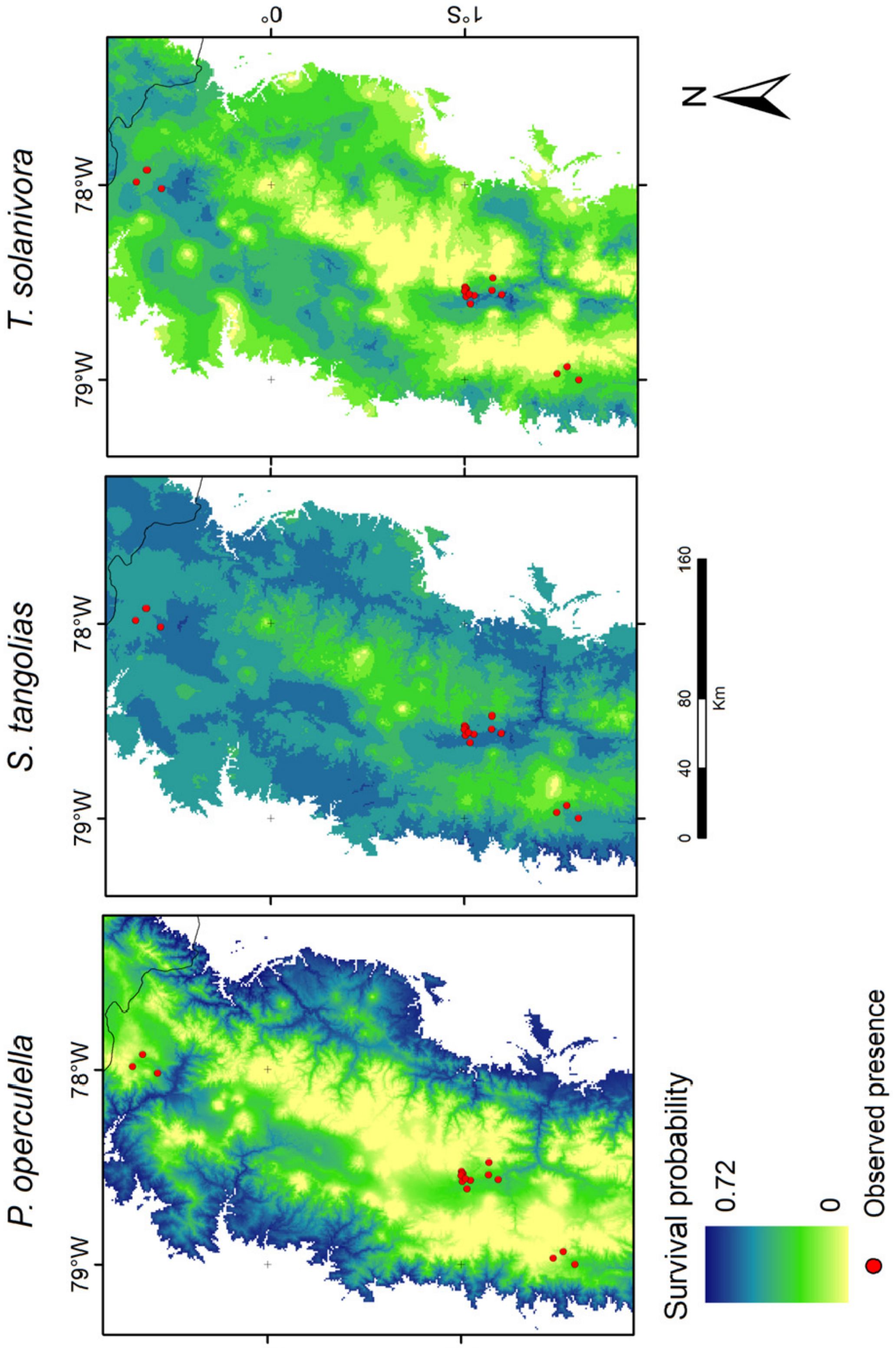

P. operculella
S. tangolias
T. solanivora
79°W
78°W
0°
1°S
0
40
80
160
Km
N
Survival probability
0.72
0
Observed presence

Fig. 4

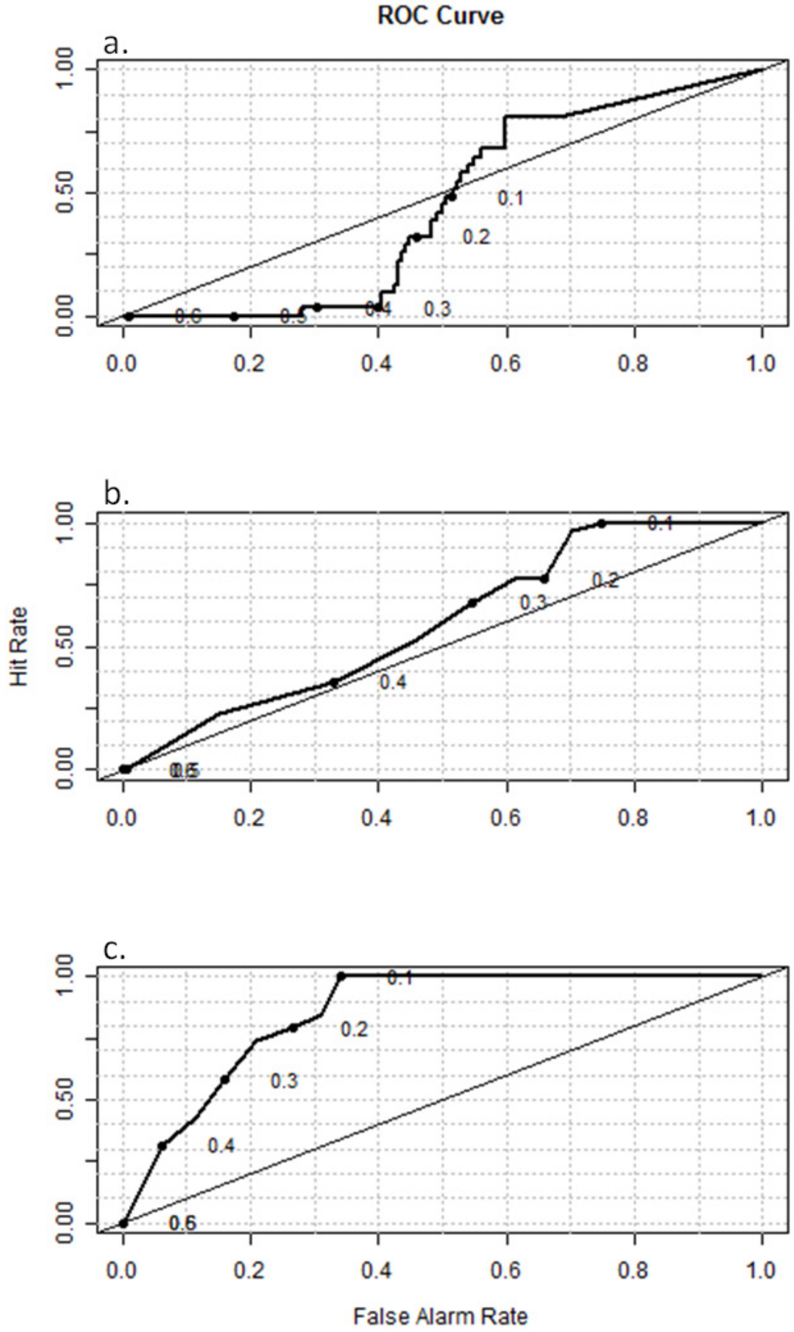

ROC Curve
a.
b.
c.
Hit Rate
False Alarm Rate
0.00
0.50
1.00
0.0
0.2
0.4
0.6
0.8
1.0
0.6
0.5
0.4
0.3
0.2
0.1
0.1
0.2
0.3
0.4
0.5
0.1
0.2
0.3
0.4
0.6

Fig. 5

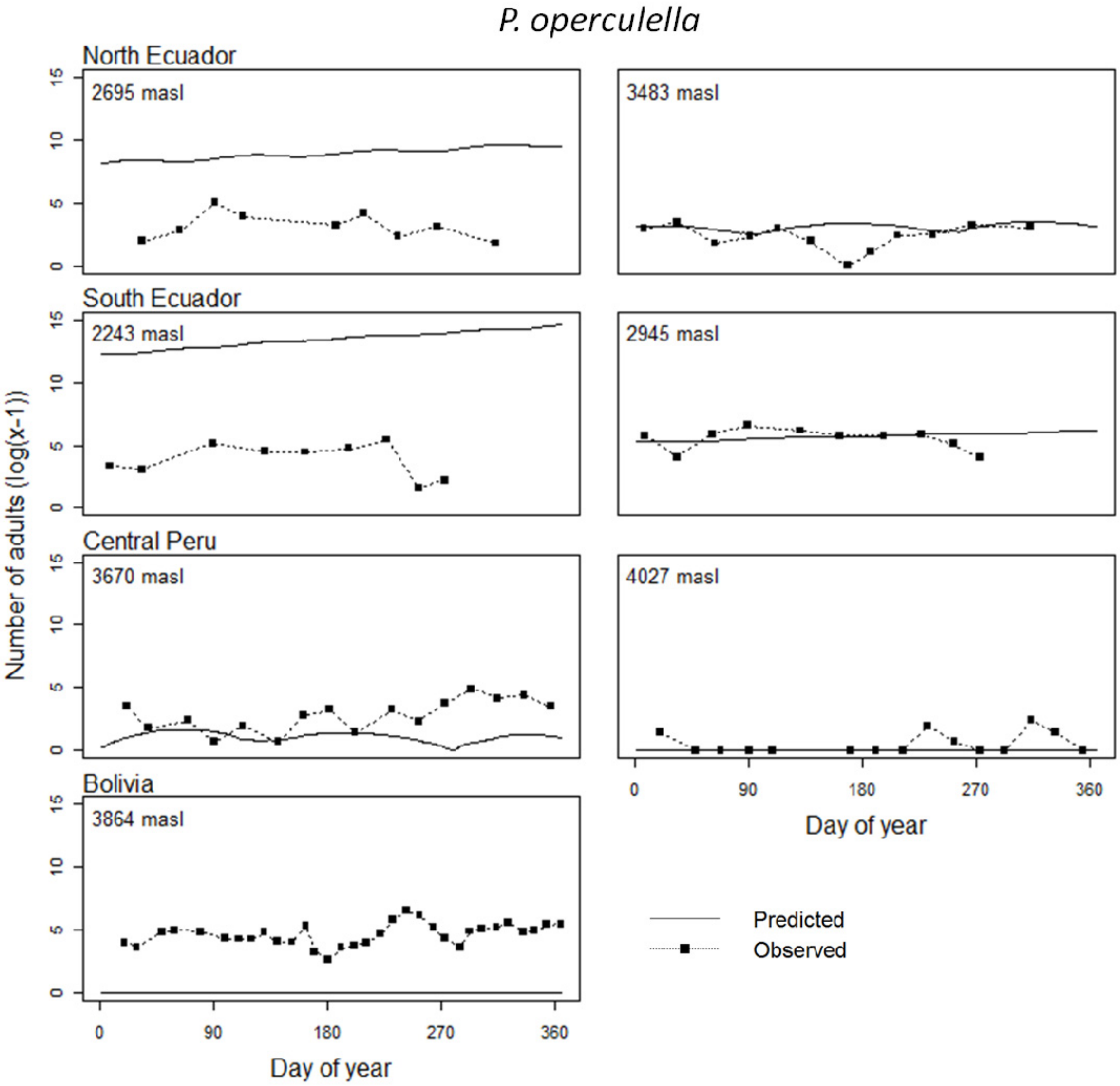

P. operculella
North Ecuador
2695 masl
3483 masl
South Ecuador
2243 masl
2945 masl
Central Peru
3670 masl
4027 masl
Bolivia
3864 masl
Number of adults (log(x-1))
0
5
10
15
0
90
180
270
360
Day of year
Predicted
Observed

Fig. 6a

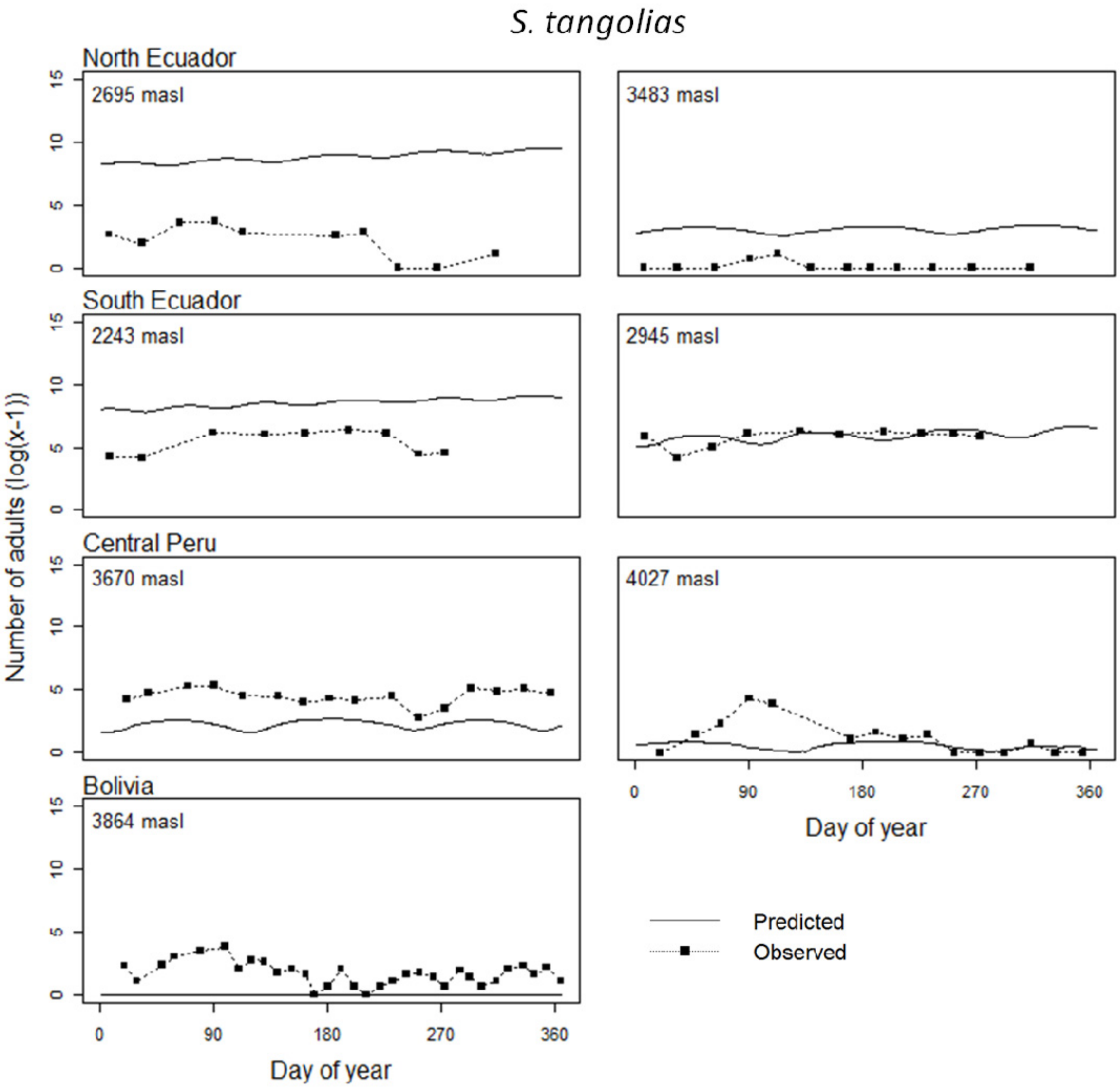

S. tangolias
North Ecuador
2695 masl
3483 masl
South Ecuador
2243 masl
2945 masl
Central Peru
3670 masl
4027 masl
Bolivia
3864 masl
Number of adults (log(x-1))
0
5
10
15
0
90
180
270
360
Day of year
Predicted
Observed

Fig. 6b

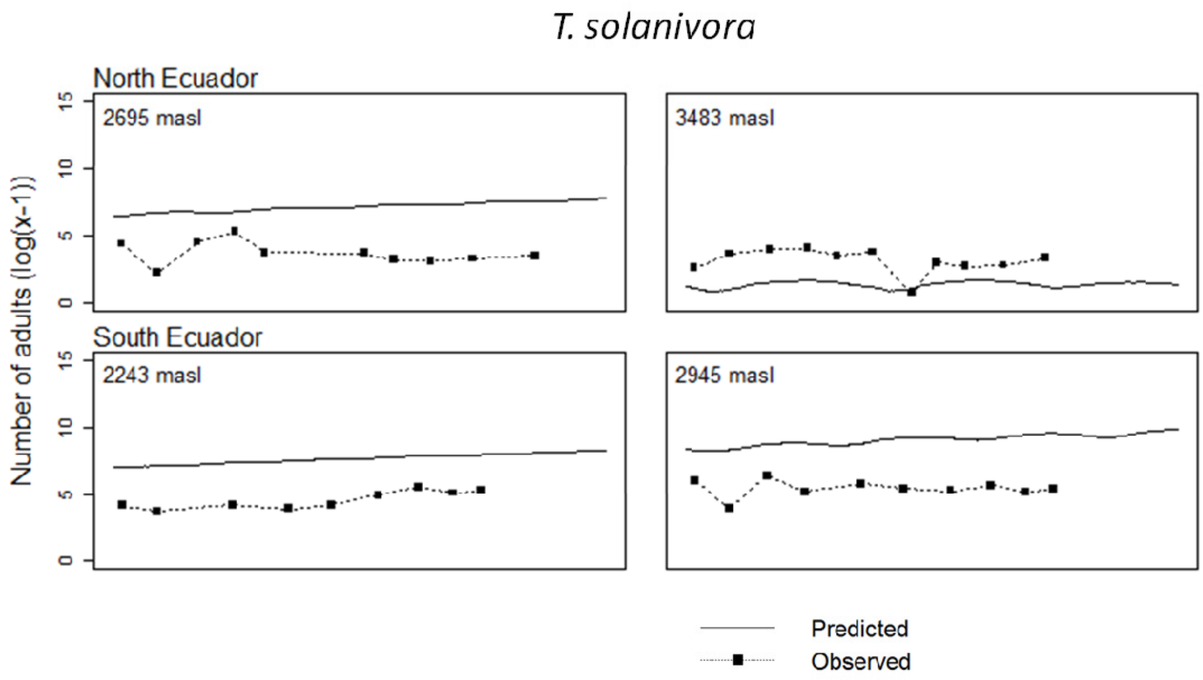

T. solanivora
North Ecuador
South Ecuador
Number of adults (log(x-1))
2695 masl
3483 masl
2243 masl
2945 masl
0
5
10
15
0
5
10
15
Predicted
Observed

Fig. 6c

P. operculella

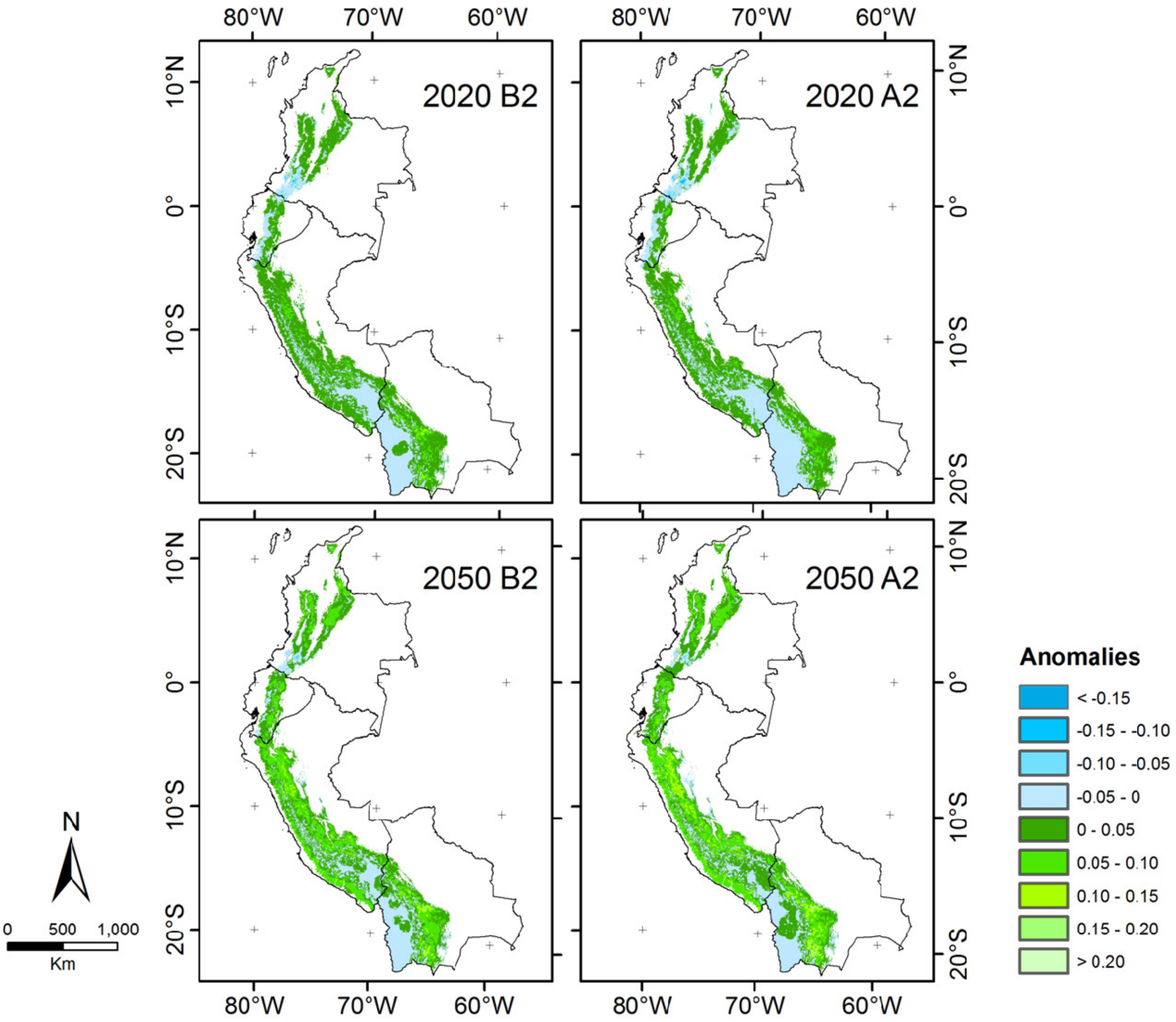


Fig. 7a

S. tangolias

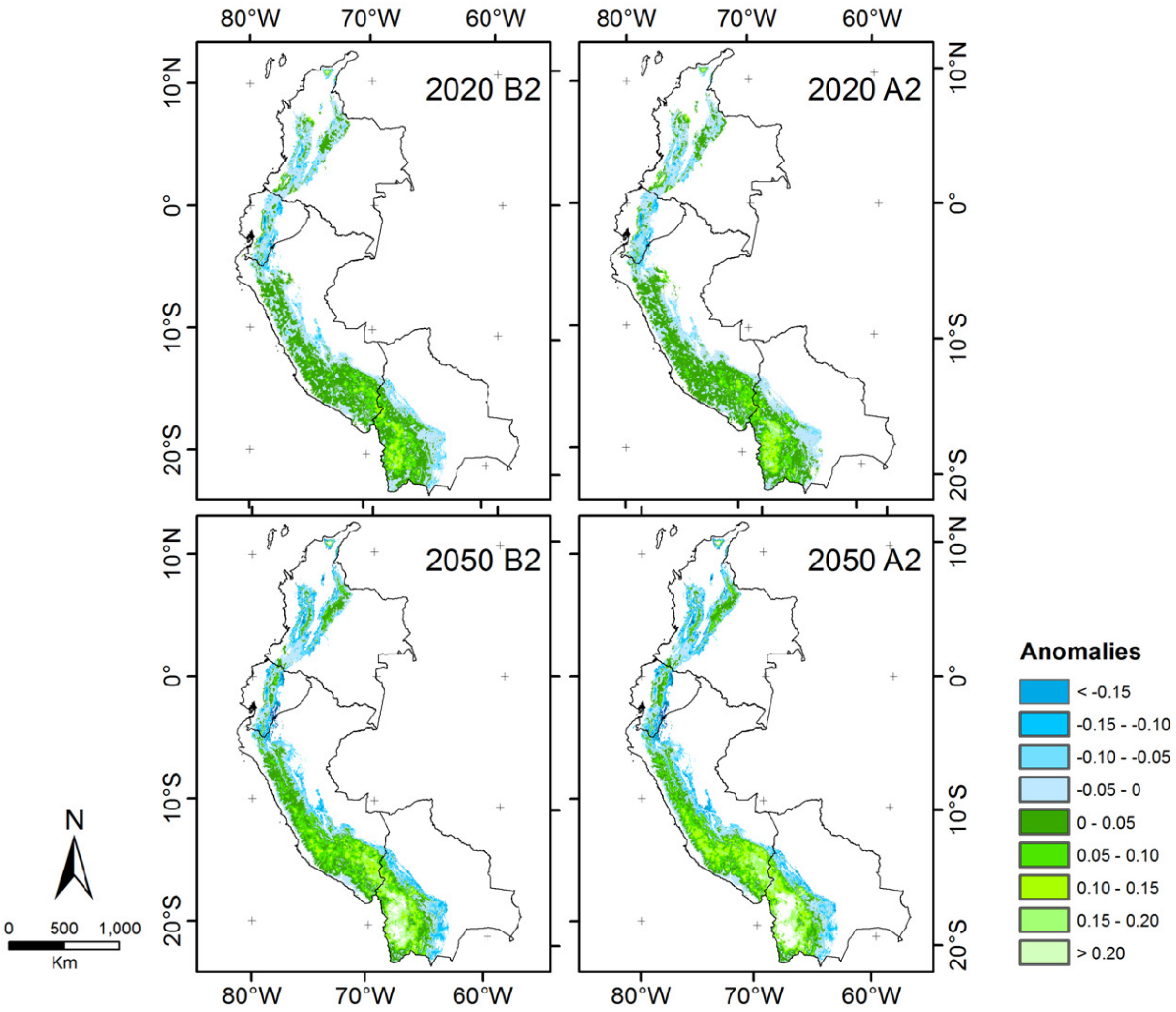


Fig. 7b

T. solanivora

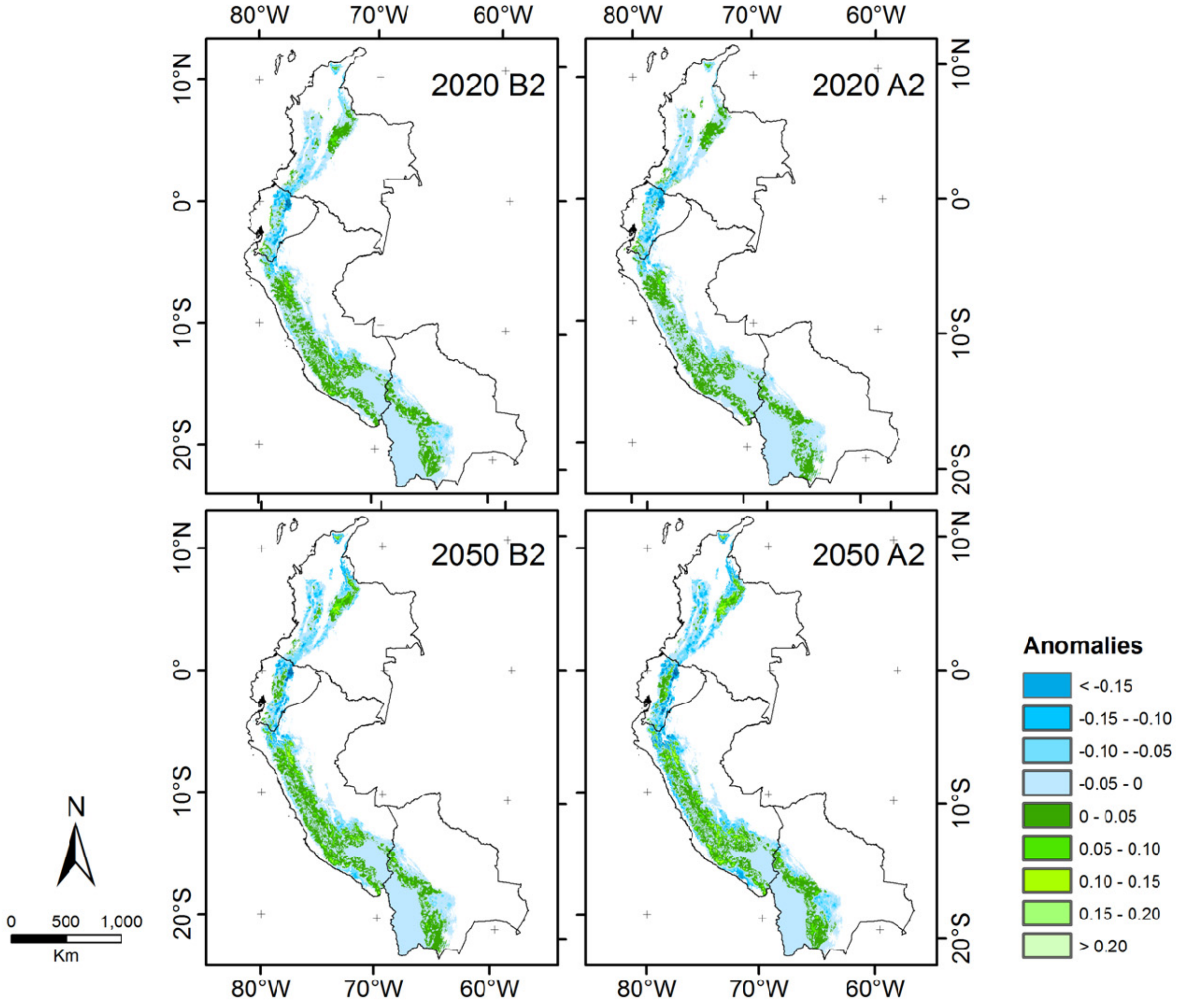


Fig. 7c

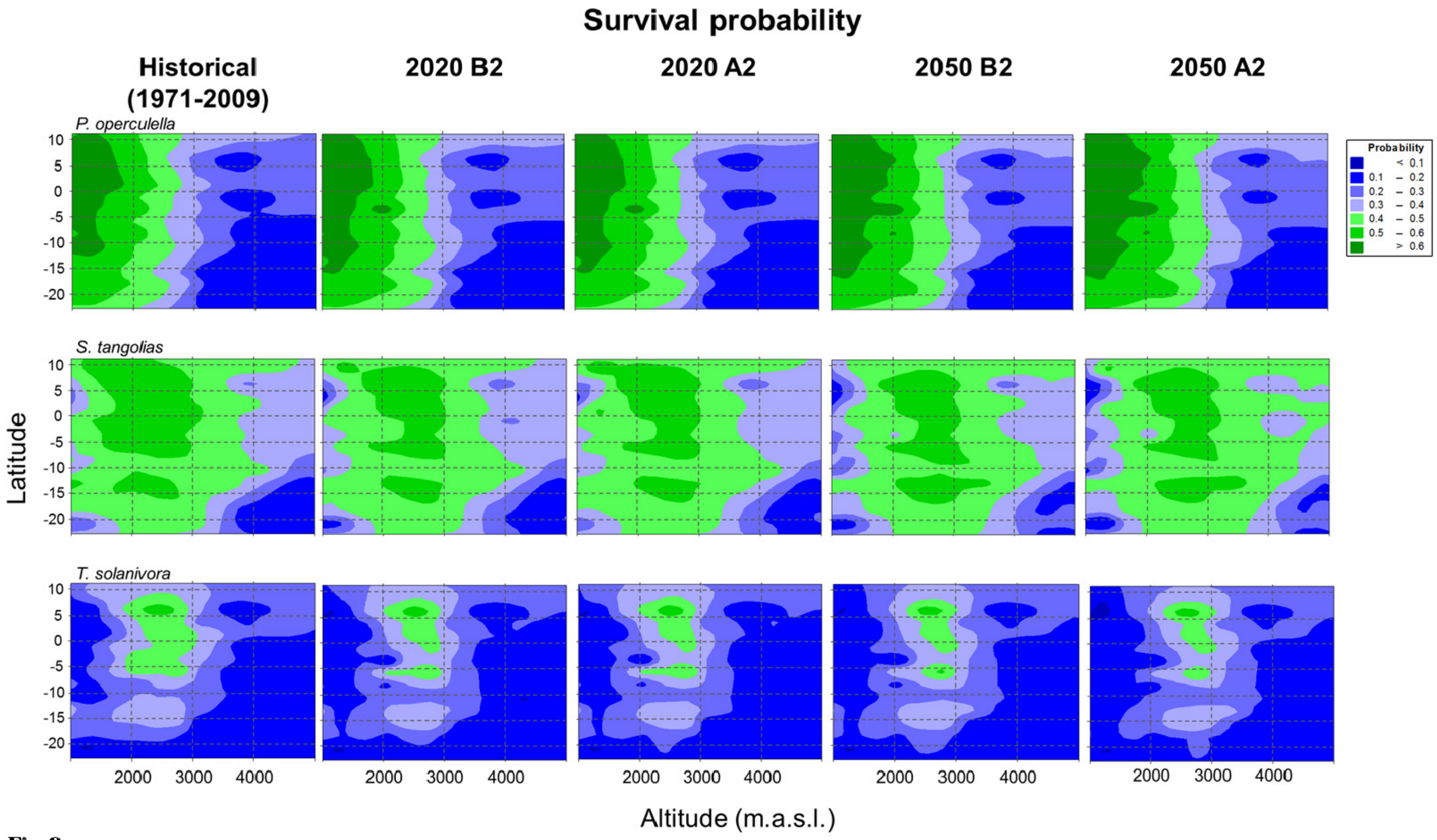

Survival probability
Historical (1971-2009)
2020 B2
2020 A2
2050 B2
2050 A2
P. operculella
S. tangolias
T. solanivora
Latitude
10
5
0
-5
-10
-15
-20
2000
3000
4000
Altitude (m.a.s.l.)
Probability
< 0.1
0.1 – 0.2
0.2 – 0.3
0.3 – 0.4
0.4 – 0.5
0.5 – 0.6
> 0.6

Fig. 8a

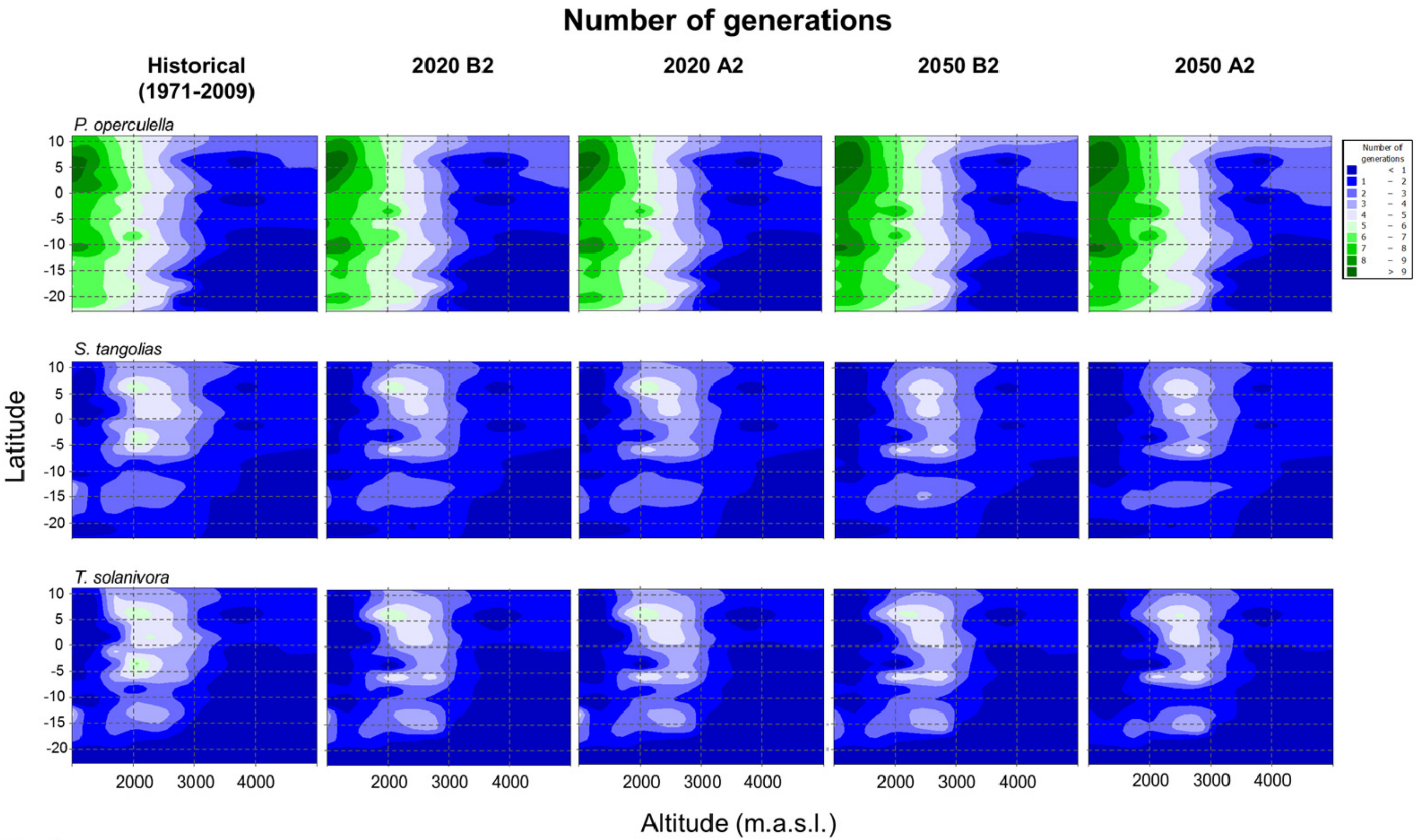

Number of generations
Historical (1971-2009)
2020 B2
2020 A2
2050 B2
2050 A2
P. operculella
S. tangolias
T. solanivora
Latitude
10
5
0
-5
-10
-15
-20
2000
3000
4000
Altitude (m.a.s.l.)
Number of generations
< 1
1 – 2
2 – 3
3 – 4
4 – 5
5 – 6
6 – 7
7 – 8
8 – 9
> 9

Fig. 8b

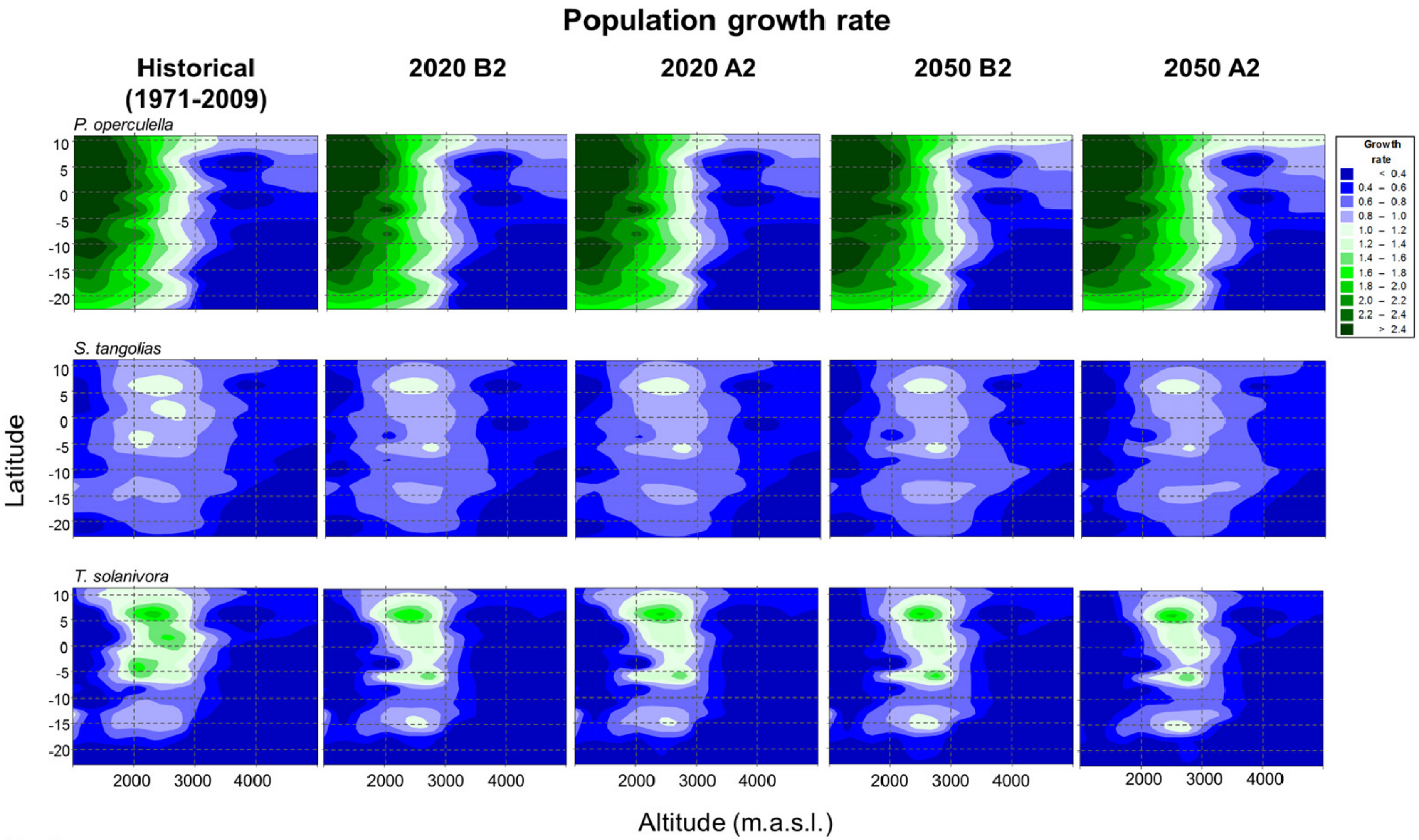

Population growth rate
Historical (1971-2009)
2020 B2
2020 A2
2050 B2
2050 A2
P. operculella
S. tangolias
T. solanivora
Latitude
10
5
0
-5
-10
-15
-20
2000
3000
4000
Altitude (m.a.s.l.)
Growth rate
< 0.4
0.4 – 0.6
0.6 – 0.8
0.8 – 1.0
1.0 – 1.2
1.2 – 1.4
1.4 – 1.6
1.6 – 1.8
1.8 – 2.0
2.0 – 2.2
2.2 – 2.4
> 2.4

Fig. 8c

APPENDICES CHAPTER 4

APPENDIX S5 – Current number of generations and population growth rate predicted by our model for the three species of PTM

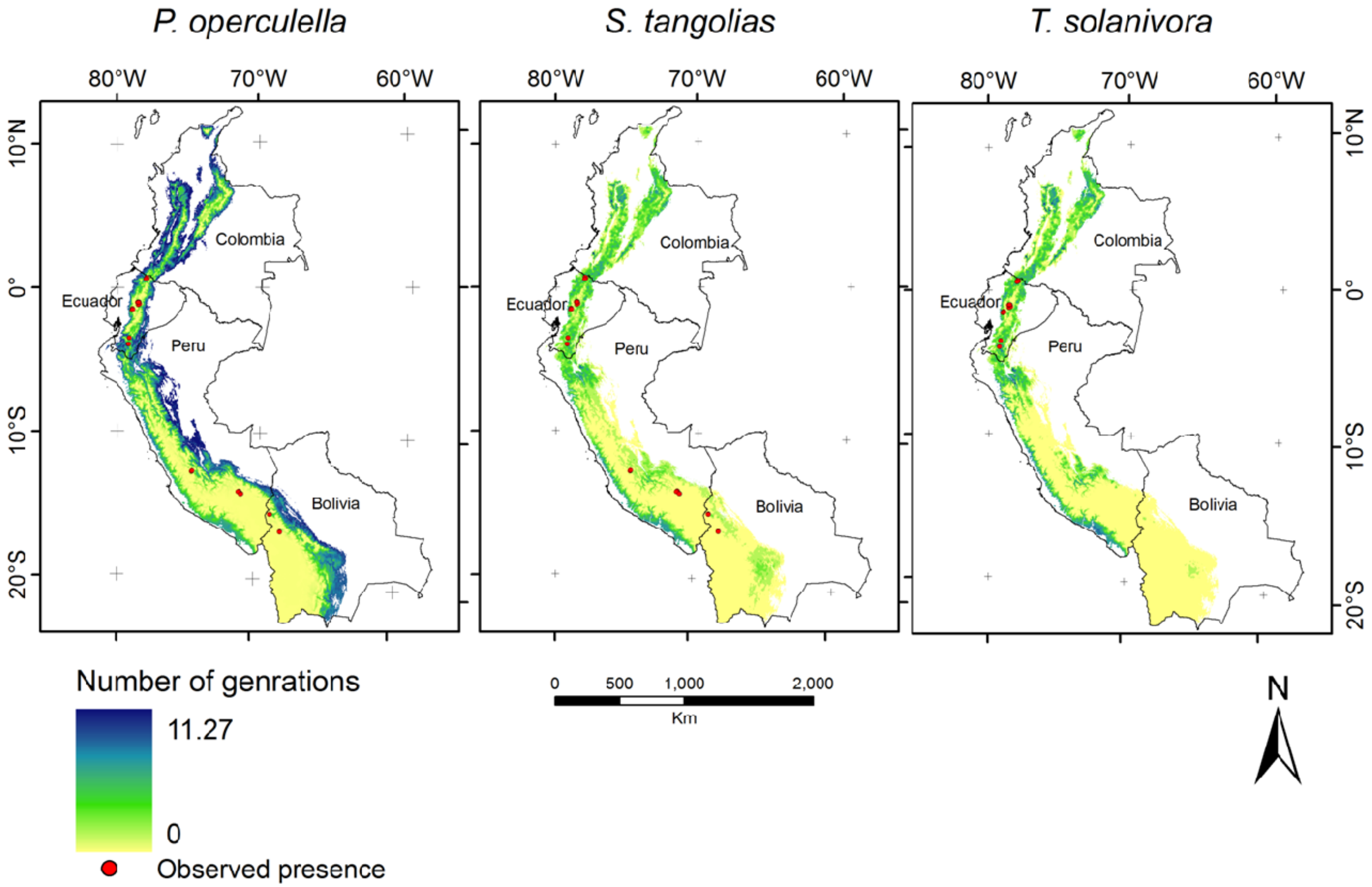


Fig. 1. Current number of generations per year

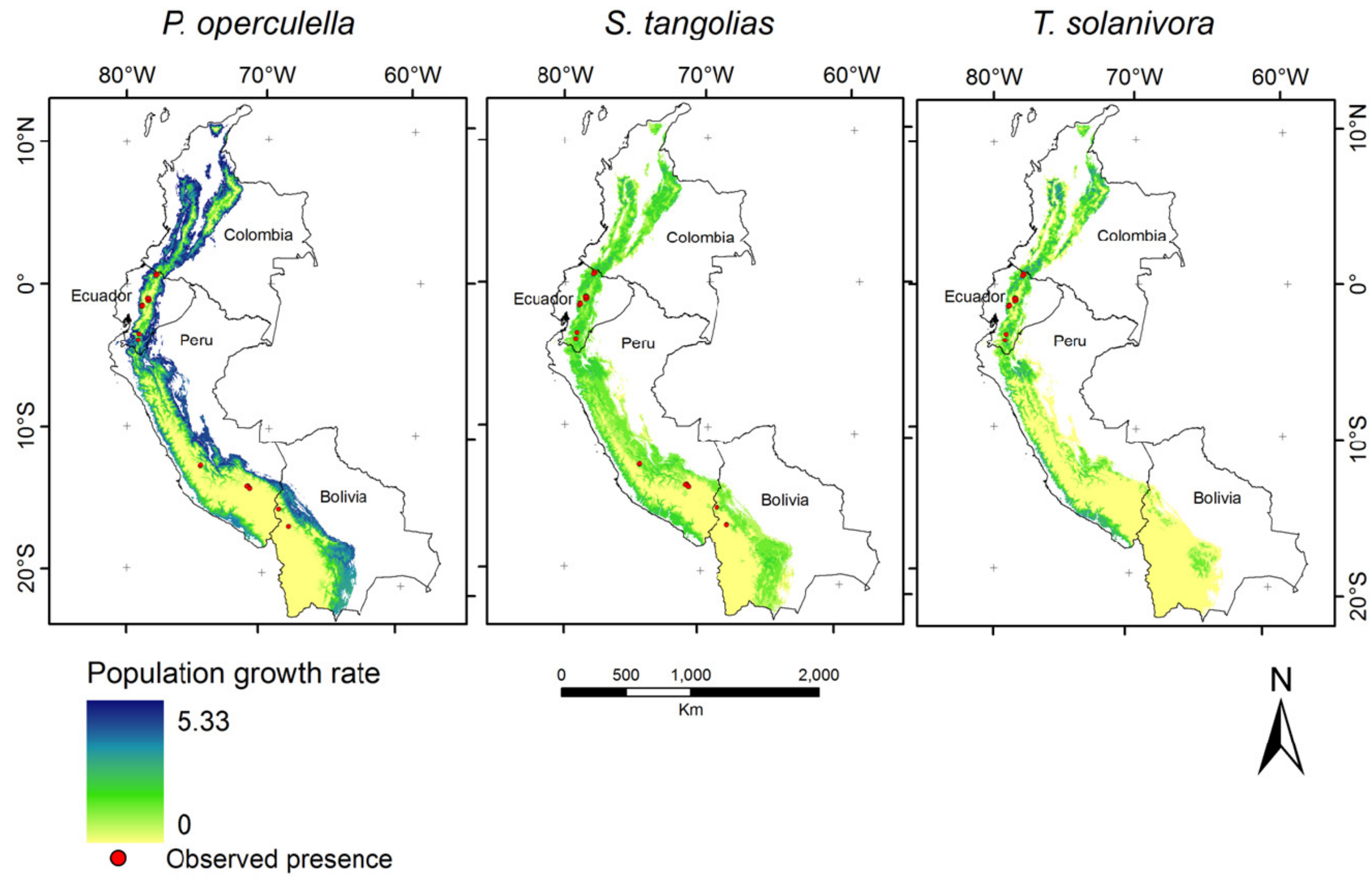
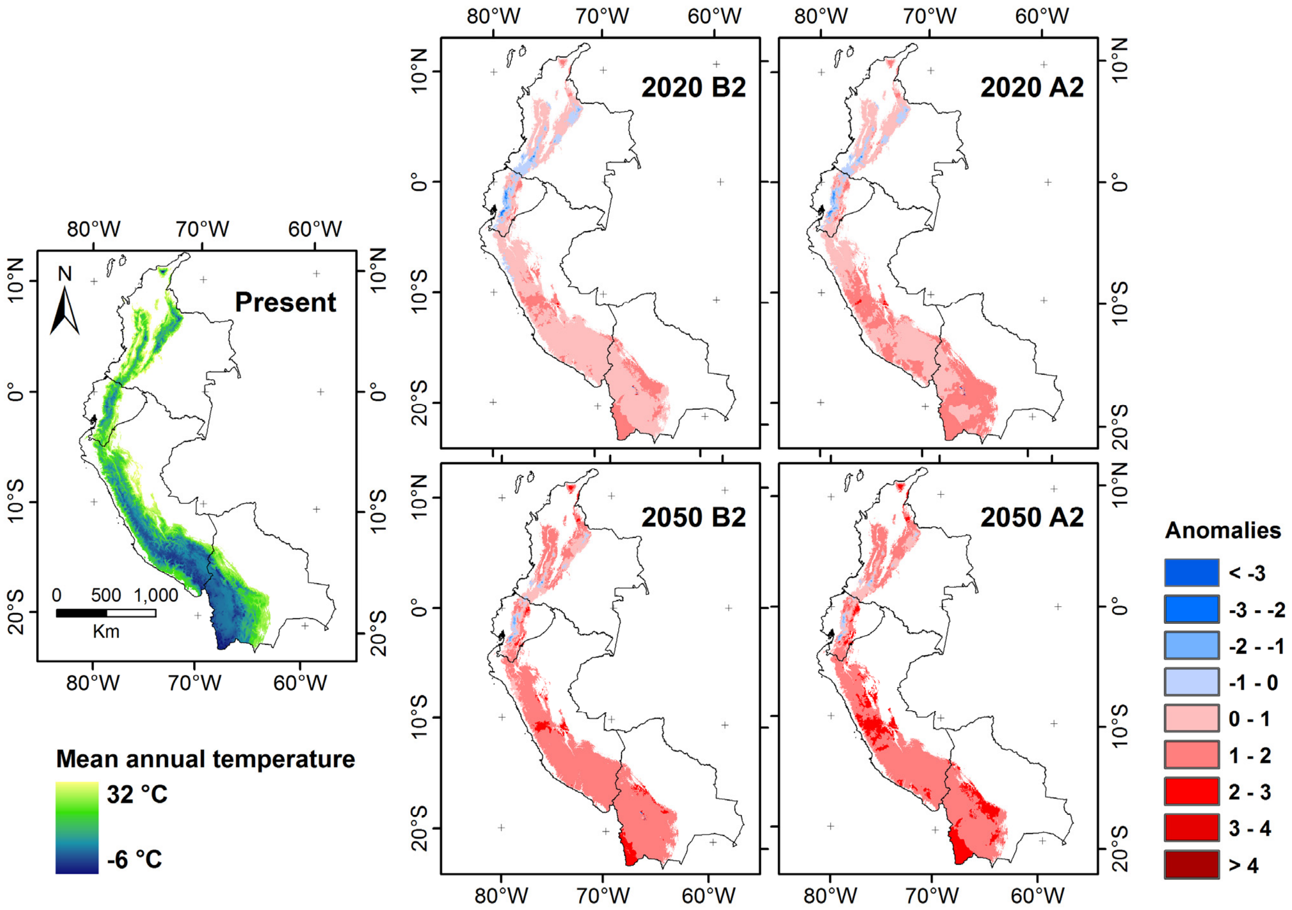


Fig. 2. Current population growth rate

APPENDIX S6– Present and future mean annual temperatures predicted by the climate model chosen for our study, for two periods in the future, 2020 and 2050 and two SRES scenarios B2 and A2.



APPENDIX S7 – Future number of generations of the three species of PTM predicted by our model for two periods in the future and two SRES scenarios.

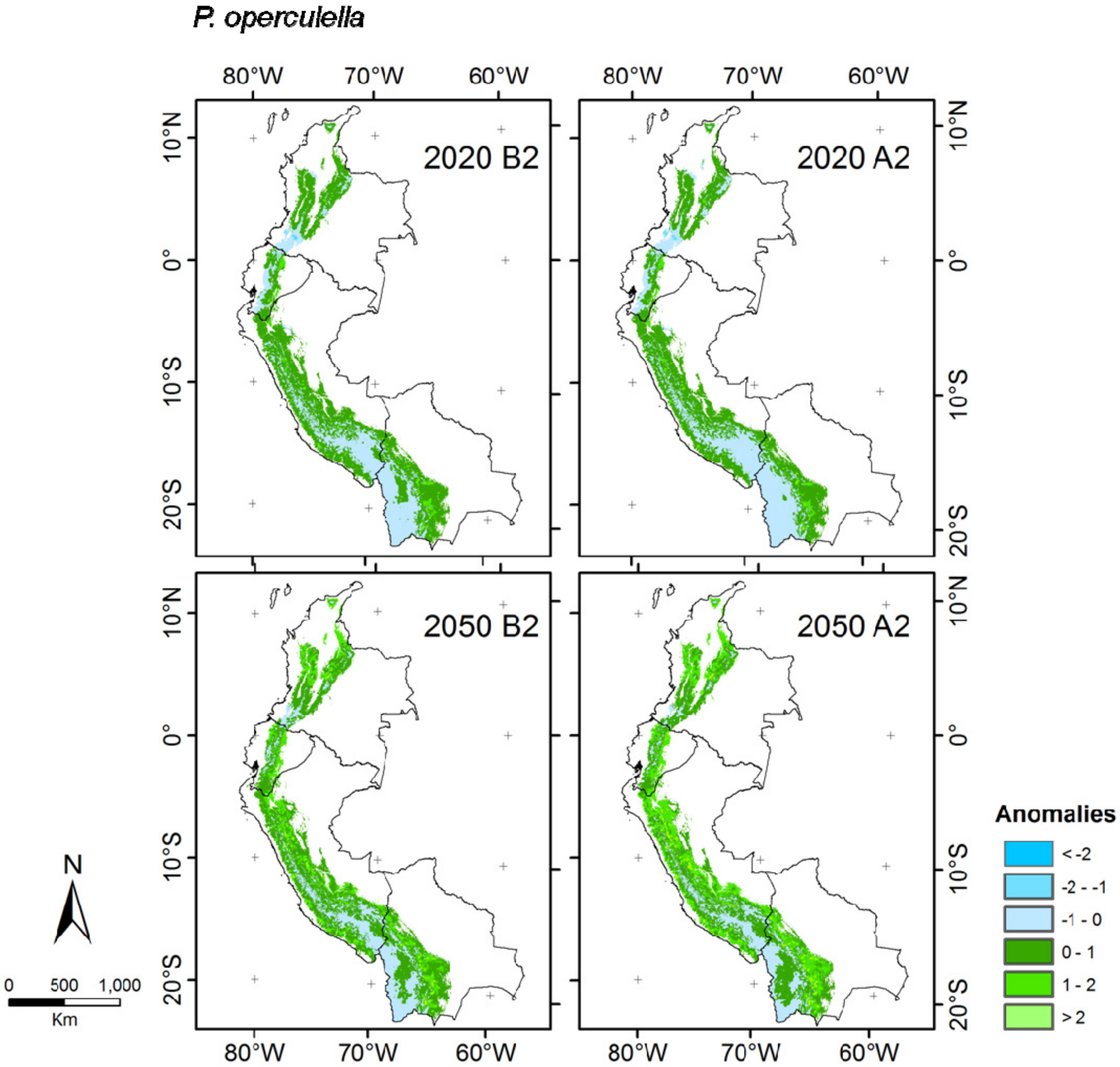


Fig. 1. Future number of generations of *P. operculella*

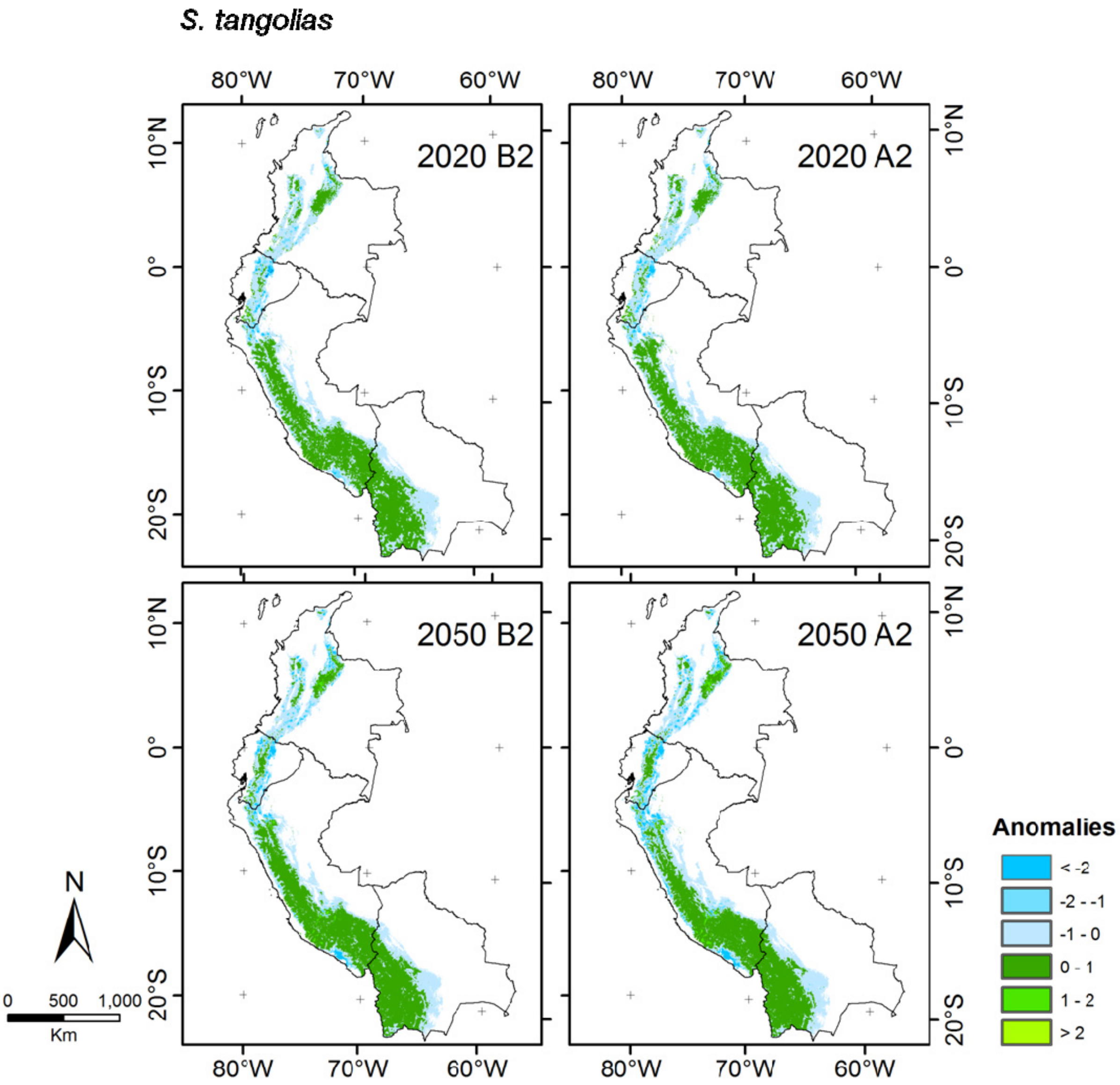


Fig. 2. Future number of generations of *S. tangolias*

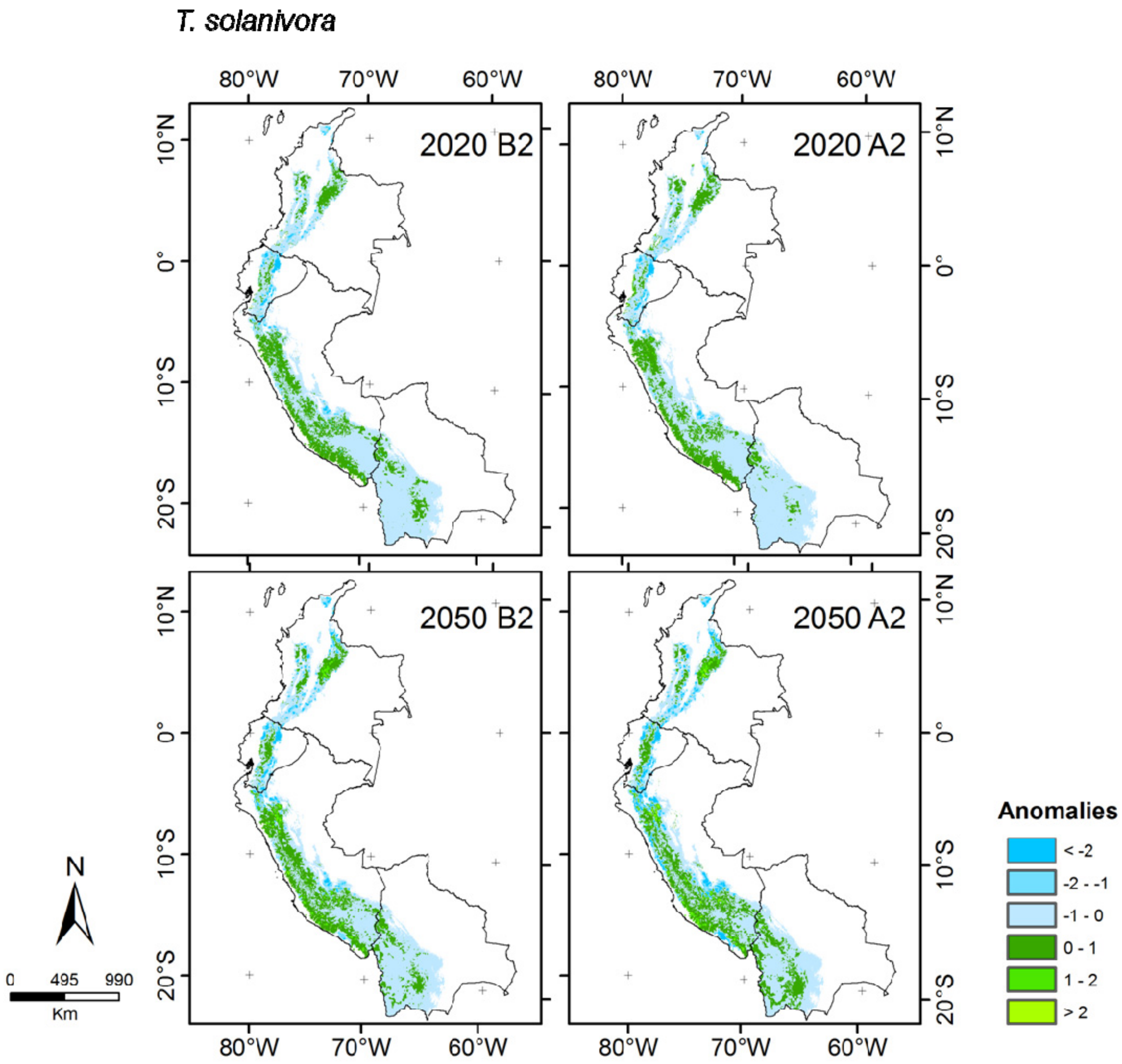


Fig. 3. Future number of generations of *T. solanivora*

APPENDIX S8 – Future population growth rate of the three species of PTM predicted by our model for two periods in the future and two SRES scenarios.

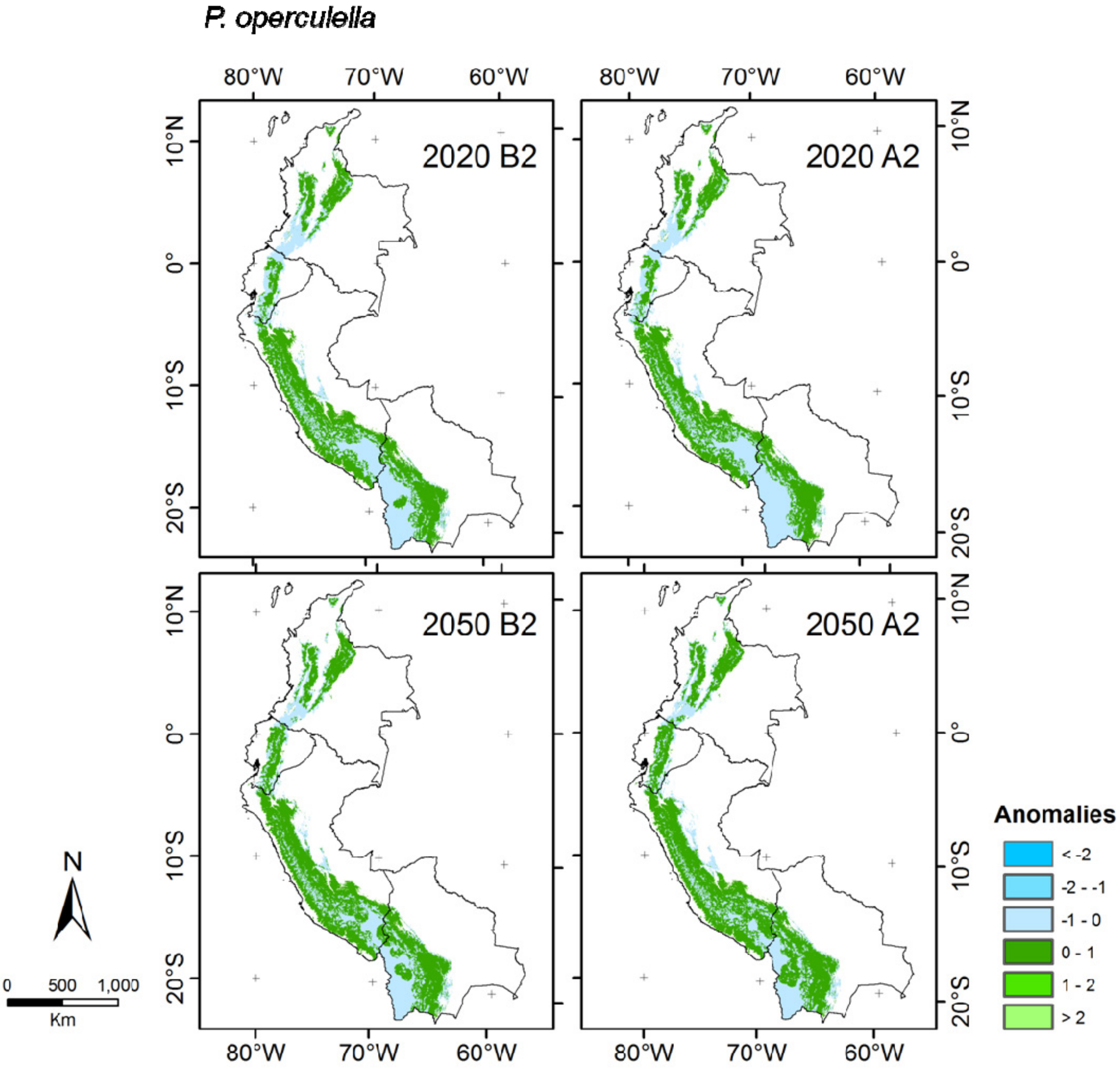


Fig. 1. Future population growth rate of *P. operculella*

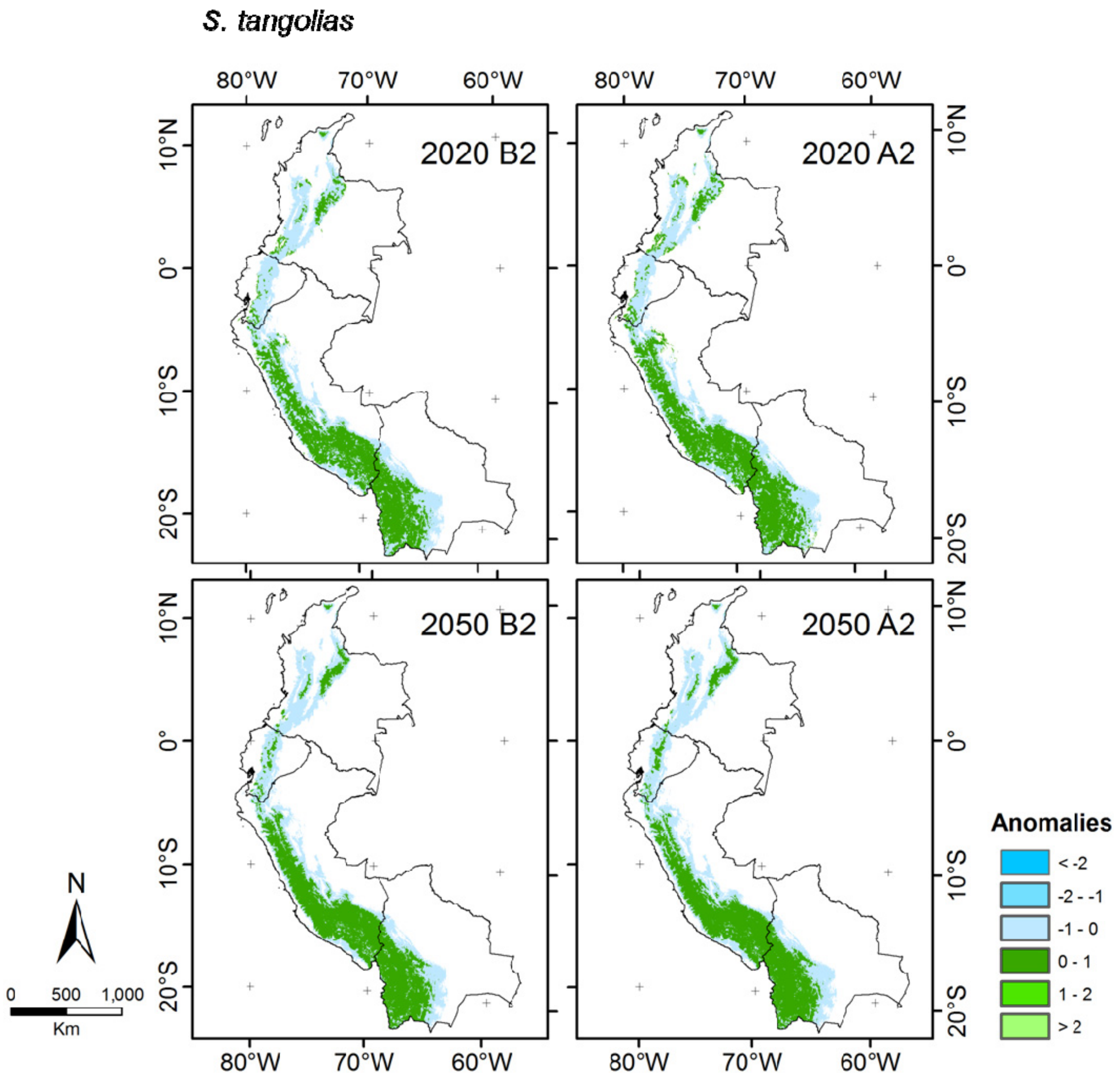


Fig. 2. Future population growth rate of *S. tangolias*

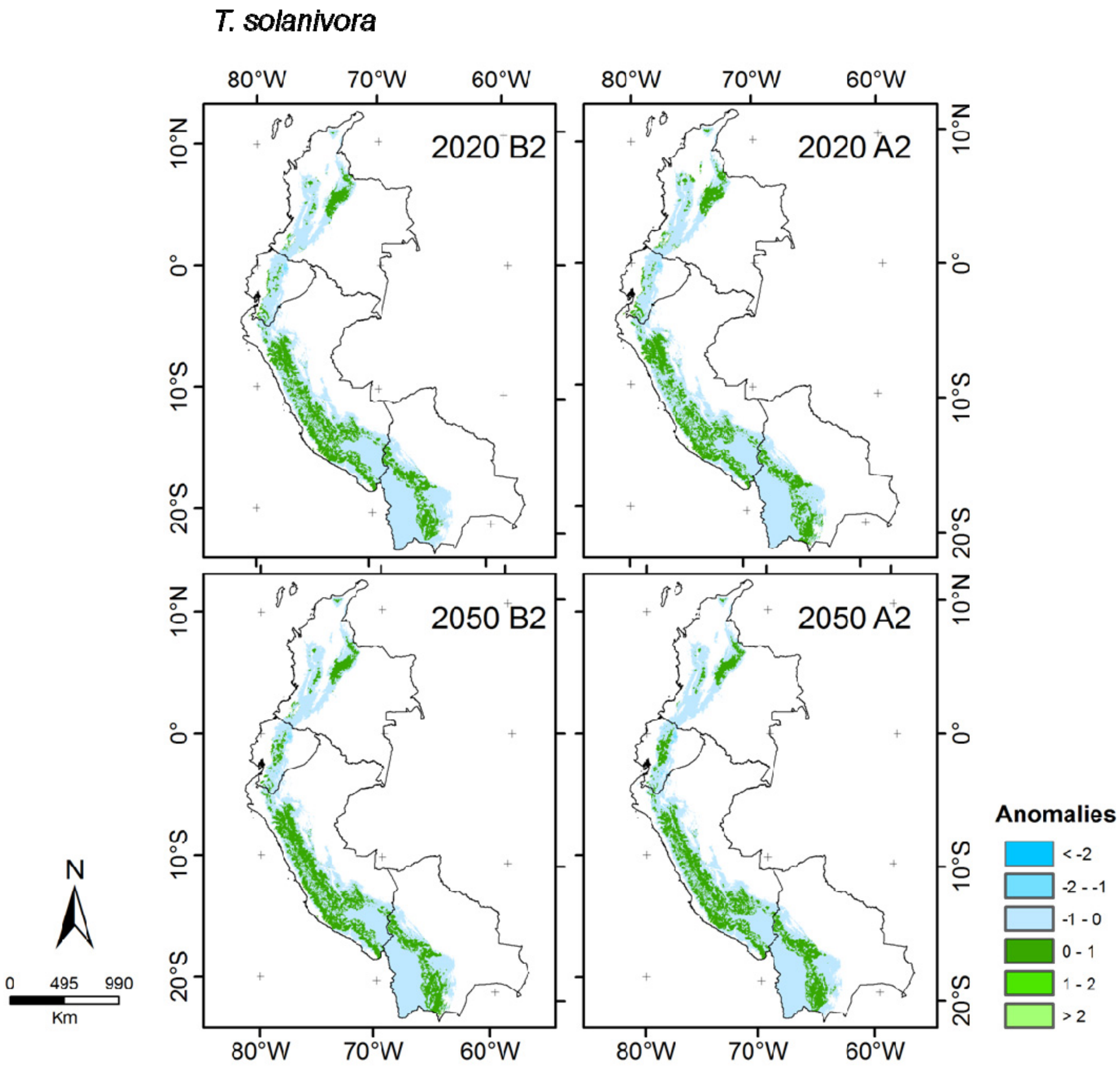
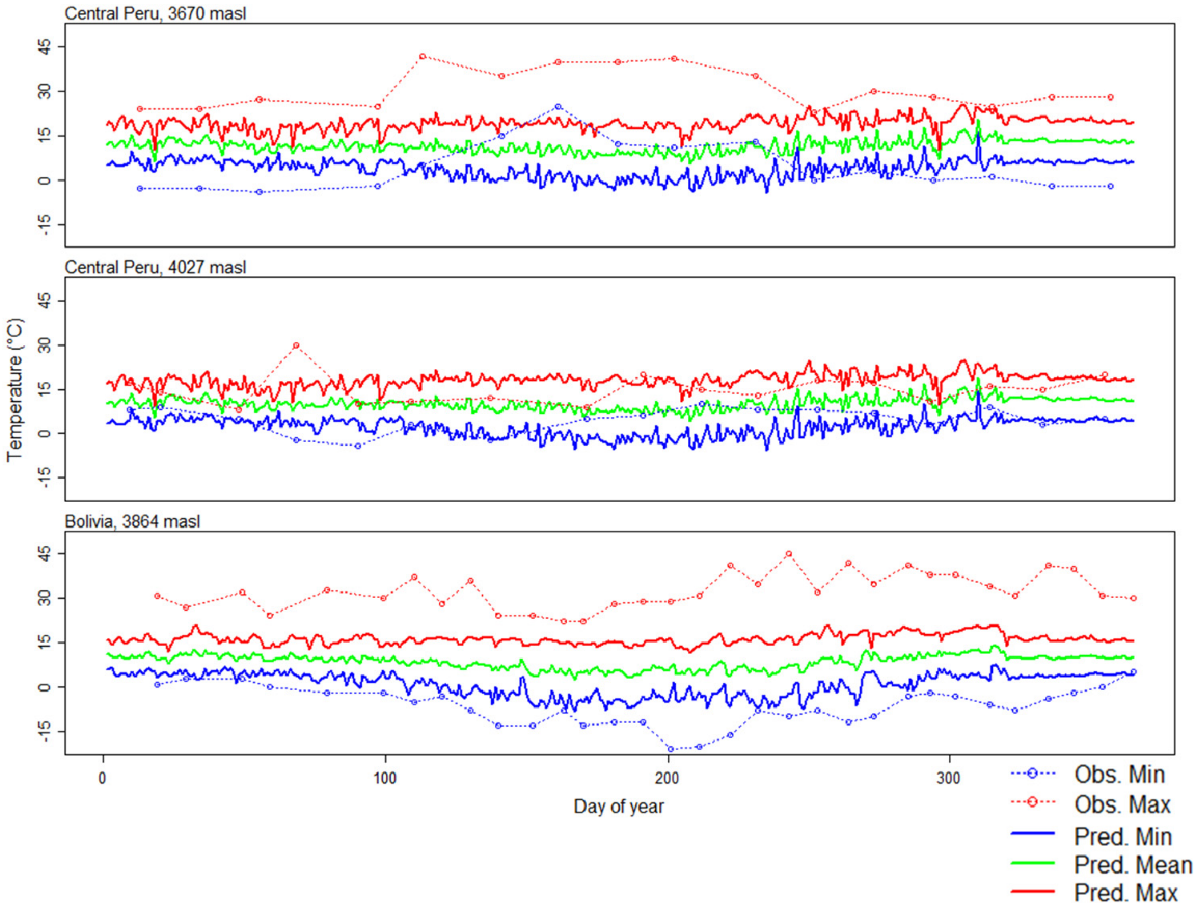


Fig. 3. Future population growth rate of *T. solanivora*

APPENDIX S9 – Predicted and observed temperatures along one year at two sites in Peru and one site in Bolivia.



DISCUSSION

CHALLENGES FOR MODELING PEST DYNAMICS IN THE TROPICAL ANDES

Ecological modeling is a valuable approach that may greatly contribute to pest management in the Tropical Andes. However, modeling in this region presents several difficulties that should be overcome for accurate and realistic simulations. One such difficulty is the high heterogeneity of the region, both environmental and social (or human-induced) (Young and Lipton 2006, Young 2009) that may influence pest invasion, establishment and propagation. Detail of both environmental and social variables included in our models was restricted by the resolution of GIS layers and data availability. Resolution of climate variables used for our cellular automaton and to construct our pest risk maps was 1 km^2. Even though resolution of the land use layer included in the automaton was higher (0.25 km^2) it did not distinguish among different types of short cycle crop and forced us to assume that the whole area with such crop had potato at the same time. These coarse resolutions and simplifications are clearly not realistic for such a heterogeneous region. Our team is currently studying heterogeneity in the Ecuadorian Andes and has found that a considerable number of different crops are cultivated within plots of 1 km^2. Temperature measurements of cultivated fields have revealed the existence of microclimates associated with the different crops (Plate 9). Crop rotation is also an important characteristic of the agricultural landscapes in the Andes which causes a temporal heterogeneity in food availability for pests. Finally, the different life stages of PTM inhabit different microhabitats and are probably exposed to different temperatures. Including all these additional sources of heterogeneity could have enhanced the realism and accuracy of our modeling approaches.

Given evidence on the influence of human activity on organisms' dynamics (Bossenbroek et al. 2007, Pitt et al. 2009, Prasad et al. 2010) we considered important to include human-induced heterogeneity into our cellular automata model. This actually suggested that moth spatio-temporal propagation is better explained when considering the influence of potato storage structures that modify local microclimate for moths and the passive transport of moth in human vehicles, than when considering natural conditions only. Since we did not dispose information on actual distribution of potato storage structures we placed such storages in our landscapes with different types of theoretical distributions (random, clumped and regular). Obtaining layers of storage distribution and including them into our cellular automaton could have allowed us to model moth propagation with more realism. We did not consider any sources of human influence to construct our pest risk maps. However, we believe that moth invasion is probably influenced by human practices at the regional scale too. Including information on human-induced heterogeneity such as crop or storage structure distribution could have also allowed us to better predict moth invasion in the region.

Another important characteristic of the North Andean region that may hinder population modeling is the extreme daily variation in temperature (Denlinger 1986). In this study we assessed the influence of such variation by simulating PTM oviposition rate under fluctuating and constant temperature regimes. We found that fluctuating temperatures caused changes in the form of the temperature-related fecundity curve, with lower number of eggs at mid-temperatures and higher number at extreme ones. We are not aware of other studies simulating oviposition rate under fluctuating temperatures. There is one study by Gilbert et al. (2004) that compared three different models to simulate Mountain Pine Beetle development and highlighted the ability of one of those models (the Extended von Foerster model) to realistically model development under varying temperatures. The absence of data on PTM oviposition dynamics under variable environments did not allow us to validate our model and to assess its ability to simulate actual oviposition dynamics. Nevertheless, our results highlighted the importance of generating realistic daily weather regimes that capture the actual levels of thermal heterogeneity, for more accurate simulations of species dynamics in heterogeneous environments.

A constant obstacle we faced during this study was the lack of data. This was for instance evidenced by the limited data sets available for modeling PTM survival probability which did not cover the entire temperature range. Deleterious effects of temperature are normally associated with temperature extremes (Angilletta 2009). Such information is of particular importance for modeling dynamics in places such as the high Andes where temperatures may approach such extremes. We therefore considered important to develop a model capable of simulating the deleterious effects of extreme temperatures given the limited data sets. Lack of data also made it difficult to validate not only our survival models but also our oviposition rate model and our pest risk maps. Dearth of information was also an issue when running our PTM population model in the Andean region. For instance, the absence of sufficient weather stations, tied to high topographic heterogeneity, made it difficult to simulate temperature realistically in some parts of the study region. This may have decreased the predictive power of our model and its ability to accurately simulate moth distribution in some parts of the region (i.e. distribution of *P. operculella* and *S. tangolias* in Bolivia). Also this model's performance was reduced by the fact that we parameterized our submodels (survival, development and oviposition) with data from a small number of populations that did not cover the entire distribution range of the species. Genetic bottlenecks (commonly associated with invasive populations) and adaptations of populations to local climatic conditions may cause responses to climate to vary among populations. Therefore, to more accurately predict species distribution across an entire region (especially one as heterogeneous as ours) models should be ideally calibrated with data from populations covering a large portion of the region.

THIS PHD AS PART OF A LARGER PROJECT

The INNOMIP project, of which this PhD project was part, is almost finalized now and has produced various important products contributing to more efficient pest management in the region. Several publications have been produced to make the project's results available to the scientific community and technicians involved in IPM. Those in collaboration with the present author are detailed bellow:

1) As an effort to better understand pest dynamics the project conducted a study about the effect of co-occurrence of two or more PTM species in potato tubers (Dangles et al. 2009, and see Appendix S10). This contribution revealed crop damage levels increase with pest diversity and that when the three species are present damage is greater than that predicted by the added effects of each species alone. This study unveiled the dangers of co-infection of the same crop by several pests, and results could later be used in our models to include effects of species interactions.

2) A simplified form of a cellular automata developed by the author to study PTM pest dynamics in an agricultural landscape (see Chapter 1 of this thesis) was integrated with an agent-based model to assess the importance of farmers' mobility and pest control knowledge on pest expansion (Rebaudo et al. 2011, and see Appendix S11). Such a coupled model was then used as an educational tool to make farmers aware of the dangers related to the pest and on the procedures they should follow to impede its

propagation. Also, a description of a simplified version of the cellular automata is available at: http://cormas.cirad.fr/en/applica/SimPolilla.htm.

3) We divulged our results to the general public and to technicians through an article published in a popular science magazine (Crespo et al. 2009, and see Appendix S12) which described our cellular automata model and through a free-distribution booklet (Carpio et al. 2011, and see Appendix S13) which described the methods for integrated pest management proposed by our project. Finally, pest risk maps developed during the present study will be made available to the public for downloading from the project's webpage. They may be used by technicians to focus their IPM efforts or their farmer training programs in areas with high (or potentially high) pest incidence.

One of the most important advantages of being part of a larger project was the availability of data on PTM and climate monitoring at a regional scale. These data are constantly being uploaded to the project's web page (www.innomip.ird.fr) and are available for download for the project collaborators. As stated before insufficient data are a common difficulty for modeling in the region. Therefore, approaches such as this one to manage and distribute data constitute important advances towards improving both knowledge about these pests' and the capacity to model their dynamics in the North Andean Region.

PERSPECTIVES

This dissertation pointed out at several lines of future research and potential applications of our modeling approaches. For example, one perspective regarding our cellular automaton is the inclusion of data on interactions between the three species of PTM (Mazoyer 2007, Dangles et al. 2009b). Such data showed that PTM may interact positively (facilitation) or negatively (competition) when inhabiting the same potato tuber, depending on the sequence of arrival to the tuber and on the species present. This could allow us to better understand and simulate pest propagation in landscapes where more than one species is present. The dynamics and influence of natural enemies, such as parasitoids could also be included in our model and could be of great help to assess the timing and placement of biological control measures. Other interesting biotic interactions that we could consider in future modeling of

PTM dynamics is the presence/absence of potato cultures (both spatial and temporal) in the region.

The high levels of human intervention in the North Andean region and the consequent changes associated with it emphasize the importance of including “social scenarios” more explicitly in future modeling approaches. For instance, the shift of the agricultural frontier towards higher altitudes demands urgent assessment of its influence on pest dynamics. Farmer practices to control pests are also a very interesting factor to take into account in models. Our team has developed an agent-based model that allows assessing the importance of farmers’ mobility and pest control knowledge on PTM expansion (Rebaudo et al. 2011). Such approaches may constitute important tools for integrated pest management programs since they may help raise awareness of farmers towards the importance of their actions on the invasion and spread of pests.

Our team is currently studying the existence of microclimates in potato cultures and their influence on PTM. This information could later be included in our models and used to enhance our comprehension of pest dynamics given this additional source of environmental heterogeneity. We are also on the process of developing a simple mechanistic model driven by air temperature regimes to simulate temperature inside storage structures. This model, along with data on potato storage structure presence, at least from some parts of the region, could be incorporated into our PTM population model or our cellular automaton to include the influence of this anthropogenic factor on moth dynamic in a more realistic fasion.

Data from climate surveys with data-loggers could be used to run our PTM population model in specific landcapes and potentially with a higher resolution. This could be quite useful for local PTM management programs. For instance, our model may help assess the most vulnerable sites to moth invasion in a small landscape where pest control measures (i.e. the application of bio-insecticides) should be prioritized. Also, it may help institutions concerned with farmer training on IPM to select areas where they should realize their training programs.

The high variability in daily temperatures observed in the region suggests the importance of developing studies about the influence of such variability on moth dynamics and on the ability of models to simulate dynamics in variable-temperature regimes (Gilbert et al. 2004). Also, more information about the species' responses to variable temperatures and on their actual distribution would improve our ability to evaluate our models.

Both approaches developed in this dissertation could also be modified to simulate dynamics of other species for which information about their temperature-related responses and invasion dynamics is available. These could serve as important tools not only for pest management purposes but also maybe for conservation issues (Griebeler and Seitz 2002).

REFERENCES

Abril, S., J. Oliveras, and C. Gomez. 2010. Effect of temperature on the development and survival of the Argentine ant, Linepithema humile. Journal of Insect Science **10**.

Adamo, S. A., and M. M. E. Lovett. 2011. Some like it hot: the effects of climate change on reproduction, immune function and disease resistance in the cricket *Gryllus texensis*. Journal of Experimental Biology **214**:1997-2004.

Allen, J. C., Y. Yang, and J. L. Knapp. 1995. Temperature effects on development and fecundity of the citrus rust mite (Acari, Eriophyidae). Environmental Entomology **24**:996-1004.

Alpatov, W. W., and R. Pearl. 1929. Experimental studies on the duration of life XII. Influence of temperature during the larval period and adult life on the duration of the life of the imago of *Drosophila melanogaster*. American Naturalist **63**:37-67.

Andrewartha, H. G., and L. C. Birch. 1960. Some Recent Contributions to the Study of the Distribution and Abundance of Insects. Annual Review of Entomology **5**:219-242.

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

Angilletta, M. J., R. B. Huey, and M. R. Frazier. 2010. Thermodynamic Effects on Organismal Performance: Is Hotter Better? Physiological and Biochemical Zoology **83**:197-206.

Angilletta, M. J., Jr. 2006. Estimating and comparing thermal performance curves. Journal of Thermal Biology **31**:541-545.

Angilletta, M. J., P. H. Niewiarowski, and C. A. Navas. 2002. The evolution of thermal physiology in ectotherms. Journal of Thermal Biology **27**:249-268.

Angilletta, M. J., T. D. Steury, and M. W. Sears. 2004. Temperature, growth rate, and body size in ectotherms: Fitting pieces of a life-history puzzle. Integrative and Comparative Biology **44**:498-509.

Arnold, C. Y. 1960. Maximum-minimum temperatures as a basic for computing heat units. Proceedings American Society for Horticultural Science **76**:682-692.

Bahrndorff, S., J. Maien, V. Loeschcke, and J. Ellers. 2009. Dynamics of heat-induced thermal stress resistance and Hsp70 expression in the springtail, *Orchesella cincta*. Functional Ecology **23**:233-239.

Bale, J. S., G. J. Masters, I. D. Hodkinson, C. Awmack, T. M. Bezemer, V. K. Brown, J. Butterfield, A. Buse, J. C. Coulson, J. Farrar, J. E. G. Good, R. Harrington, S. Hartley, T. H. Jones, R. L. Lindroth, M. C. Press, I. Symrnioudis, A. D. Watt, and J. B.

Whittaker. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Global Change Biology **8**:1-16.

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

Berger, D., R. Walters, and K. Gotthard. 2008. What limits insect fecundity? Body size- and temperature-dependent egg maturation and oviposition in a butterfly. Functional Ecology **22**:523-529.

Berrigan, D. 2000. Correlations between measures of thermal stress resistance within and between species. Oikos **89**:301-304.

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

Bossenbroek, J. M., L. E. Johnson, B. Peters, and D. M. Lodge. 2007. Forecasting the expansion of zebra mussels in the United States. Conservation Biology **21**:800-810.

Bradley, R. S., M. Vuille, H. F. Diaz, and W. Vergara. 2006. Threats to water supplies in the tropical Andes. Science **312**:1755-1756.

Bradshaw, W. E., and C. M. Holzapfel. 2006. Climate change - Evolutionary response to rapid climate change. Science **312**:1477-1478.

Brent, C. S. 2010. Reproduction of the western tarnished plant bug, *Lygus hesperus*, in relation to age, gonadal activity and mating status. Journal of Insect Physiology **56**:28-34.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. Ecology **85**:1771-1789.

Buffoni, G., and S. Pasquali. 2010. Individual-based models for stage structured populations: formulation of "no regression" development equations. Journal of Mathematical Biology **60**:831-848.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer, New York.

Butler, G. D. J., R. E. Stinner, and G. L. Greene. 1976. Application of a Thermodynamic Model for the Development of Larvae of the Cabbage Looper (Lepidoptera: Noctuidae) at Fluctuating Temperatures. The Florida Entomologist **59**:165-169

Buytaert, W. B. W., M. Vuille, A. Dewulf, R. Urrutia, A. Karmalkar, and R. Celleri. 2010. Uncertainties in climate change projections and regional downscaling in the tropical

Andes: implications for water resources management. Hydrology and Earth System Sciences **14**:1247-1258.

Cacho, O. J., D. Spring, S. Hester, and R. Mac Nally. 2010. Allocating surveillance effort in the management of invasive species: A spatially-explicit model. Environmental Modelling and Software **25**:444-454.

Cadotte, M., S. McMahon, and T. Fukami. 2006. Conceptual ecology and invasion biology: reciprocal approaches to nature. Springer Verlag, Dordretch, The Netherlands.

Candolle, A. P. d. 1855. Geographique botanique, raisonnée. Masson, Paris.

Carpio, C., V. Crespo-Perez, M. Herrera, A. Barragán, F. Rebaudo, and O. Dangles. 2011. Innovaciones para el manejo de plagas en los Andes. PUCE-IRD-Fundacion McKnight, Quito.

Carrasco, L. R., J. D. Mumford, A. MacLeod, T. Harwood, G. Grabenweger, A. W. Leach, J. D. Knight, and R. H. A. Baker. 2010. Unveiling human-assisted dispersal mechanisms in invasive alien insects: Integration of spatial stochastic simulation and phenology models. Ecological Modelling **221**:2068-2075.

Carrillo, M. A., G. E. Heimpel, R. D. Moon, C. A. Cannon, and W. D. Hutchison. 2005. Cold hardiness of *Habrobracon hebetor* (Say) (Hymenoptera : Braconidae), a parasitoid of pyralid moths. Journal of Insect Physiology **51**:759-768.

Choi, Y. H., D. A. Bohan, R. P. J. Potting, M. A. Semenov, and D. M. Glen. 2006. Individual based model of slug population and spatial dynamics. Ecological Modelling **190**:336-350.

Cloudsley-Thompson, J. L. 1956. Studies in diurnal rhythms. VI. Bioclimatic observations in Tunisia and their significance in relation to the physiology of the fauna, especially woodlice, centipedes, scorpions and beetles. Annals and Magazine of Natural History **9**:305-329.

Cook, W. C. 1932. Insects and climate. Ecology **13**:96-99.

Crespo, V., F. Rebaudo, and O. Dangles. 2009. Modelando la propagación de plagas invasoras. Nuestra Ciencia **11**:18-21.

Curry, G. L., R. M. Feldman, and P. J. H. Sharpe. 1978. Foundations of stochastic development. Journal of Theoretical Biology **74**:397-410.

Dangles, O., A. Barragan, R. E. Cardenas, G. Onore, and C. Keil. 2009a. Entomology in Ecuador: Recent developments and future challenges. Annales de la Société Entomologique de France **45**:424-436.

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

Dangles, O., C. Carpio, M. Villares, F. Yumisaca, B. Liger, F. Rebaudo, and J. F. Silvain. 2010. Community-Based Participatory Research Helps Farmers and Scientists to Manage Invasive Pests in the Ecuadorian Andes. AMBIO. **39**:325-335.

Dangles, O., V. Mesias, V. Crespo-Perez, and J. F. Silvain. 2009b. Crop damage increases with pest species diversity: evidence from potato tuber moths in the tropical Andes. Journal of Applied Ecology **46**:1115-1121.

Davidson, J. 1944. On the Relationship between Temperature and Rate of Development of Insects at Constant Temperatures. Journal of Animal Ecology **13**:26-38.

Davis, J. A., E. B. Radcliffe, and D. W. Ragsdale. 2006. Effects of high and fluctuating temperatures on *Myzus persicae* (Hemiptera : Aphididae). Environmental Entomology **35**:1461-1468.

Denlinger, D. L. 1986. Dormancy in Tropical Insects. Annual Review of Entomology **31**:239-264.

Dennis, C. A. 1938. The distribution of ant species in tennessee with reference to ecological factors. Annals of the Entomological Society of America **31**:267-308.

Devaux, A., M. Ordinola, A. Hibon, and R. Flores. 2010. El sector papa en la región andina: Diagnóstico y elementos para una visión estratégica (Bolivia, Ecuador y Perú). Centro Internacional de la Papa.

Drent, J. 2002. Temperature responses in larvae of *Macoma balthica* from a northerly and southerly population of the European distribution range. Journal of Experimental Marine Biology and Ecology **275**:117-129.

Drooz, A. T., and H. T. Schreuder. 1972. Elm Spanworm: Models of Eclosion as Related to Temperature and Relative Humidity in the Laboratory. Environmental Entomology **1**:582-588.

EPPO. 2005. Data sheets on quarantined pests, *Tecia solanivora*. Bulletin OEPP/EPPO **35**:399-401.

FAO. 2011. Country briefs. FAO.

Gamboa, M., and A. Notz. 1990. Influencia de la temperatura en el desarrollo y oviposición de *Phthorimaea operculella* (Lepidoptera: Gelechiidae). Revsita de la Facultad de Agronomia (Maracay) **16**:231-244.

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

Gilchrist, G. W. 1995. Specialists and Generalists in Changing Environments .1. Fitness Landscapes of Thermal Sensitivity. American Naturalist **146**:252-270.

Goslee, S. C., D. P. C. Peters, and K. G. Beck. 2006. Spatial prediction of invasion success across heterogeneous landscapes using an individual-based model. Biological Invasions **8**:193-200.

Griebeler, E. M., and A. Seitz. 2002. An individual based model for the conservation of the endangered Large Blue Butterfly, *Maculinea arion* (Lepidoptera : Lycaenidae). Ecological Modelling **156**:43-60.

Grimbacher, P. S., and N. E. Stork. 2009. Seasonality of a Diverse Beetle Assemblage Inhabiting Lowland Tropical Rain Forest in Australia. Biotropica **41**:328-337.

Gutiérrez, J. A., J. D. Krenz, and N. R. Ibargüengoytía. 2010. Effect of altitude on thermal responses of *Liolaemus pictus argentinus* in Argentina. Journal of Thermal Biology **35**:332-337.

Hagen, S. B., J. U. Jepsen, R. A. Ims, and N. G. Yoccoz. 2007. Shifting altitudinal distribution of outbreak zones of winter moth Operophtera brumata in sub-arctic birch forest: a response to recent climate warming? Ecography **30**:299-307.

Hance, T., J. van Baaren, P. Vernon, and G. Boivin. 2007. Impact of extreme temperatures on parasitoids in a climate change perspective. Pages 107-126 Annual Review of Entomology.

Hanski, I., J. Alho, and A. Moilanen. 2000. Estimating the parameters of survival and migration of individuals in metapopulations. Ecology **81**:239-251.

Harris, C. M., K. J. Park, R. Atkinson, C. Edwards, and J. M. J. Travis. 2009. Invasive species control: Incorporating demographic data and seed dispersal into a management model for *Rhododendron ponticum*. Ecological Informatics **4**:226-233.

Herben, T., Z. Munzbergova, M. Milden, J. Ehrlen, S. A. O. Cousins, and O. Eriksson. 2006. Long-term spatial dynamics of *Succisa pratensis* in a changing rural landscape: linking dynamical modelling with historical maps. Journal of Ecology **94**:131-143.

Hercus, M. J., D. Berrigan, M. W. Blows, A. Magiafoglou, and A. A. Hoffmann. 2000. Resistance to temperature extremes between and within life cycle stages in *Drosophila* *serrata*, *D. birchii* and their hybrids: intraspecific and interspecific comparisons. Biological Journal of the Linnean Society **71**:403-416.

Hilbert, D. W., and J. A. Logan. 1983. Empirical model of nymphal development for the migratory grasshopper, *Melanoplus sanguinipes* (Orthoptera, Acrididae). Environmental Entomology **12**:1-5.

Hochachka, P. W., and G. N. Somero. 1984. Biochemical adaptation, 1st ed. Princeton University Press, Princeton.

Hochochka, P. W., and G. N. Somero. 2000. Biochemical Adaptation. Oxford University Press, Oxford.

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

Huey, R. B., and P. E. Hertz. 1984. Is a jack-of-all-temperatures a master of none? Evolution **38**:441-444.

Huey, R. B., and J. G. Kingsolver. 1989. Evolution of thermal sensitivity of ectotherm performance. Trends in Ecology & Evolution **4**:131-135.

Huey, R. B., and R. D. Stevenson. 1979. Integrating thermal physiology and ecology of ectotherms: A discussion of approaches. American Zoologist **19**:357-366.

Huffaker, C. B. 1944. The temperature relations of the immature stages of the malarial mosquito, *Anopheles quadrimaculatus* Say, with a comparison of the developmental power of constant and variable temperatures in insect metabolism. Annals of the Entomological Society of America **37**:1-27.

Hunter, C. M., and H. Caswell. 2005. The use of the vec-permutation matrix in spatial matrix population models. Ecological Modelling **188**:15-21.

IPCC. 2007. Summary for Policymakers. Cambridge University Press, Cambridge.

Janisch, E. 1932. The influence of temperature on the life-history of insects. Transactions of the Entomological Society of London **80**:137-168.

Jarvis, C. H., and R. H. A. Baker. 2001. Risk assessment for nonindigenous pests: 1. Mapping the outputs of phenology models to assess the likelihood of establishment. Diversity and Distributions **7**:223-235.

Jongejans, E., O. Skarpaas, and K. Shea. 2008. Dispersal, demography and spatial population models for conservation and control management. Perspect Plant Ecol Evol Syst. **9**:153-170.

Karl, I., S. A. Janowitz, and K. Fischer. 2008. Altitudinal life-history variation and thermal adaptation in the copper butterfly *Lycaena tityrus*. Oikos **117**:778-788.

Kearney, M., W. P. Porter, C. Williams, S. Ritchie, and A. A. Hoffmann. 2009. Integrating biophysical models and evolutionary theory to predict climatic impacts on species' ranges: the dengue mosquito *Aedes aegypti* in Australia. Functional Ecology **23**:528-538.

Keasar, T., A. Kalish, O. Becher, and S. Steinberg. 2005. Spatial and temporal dynamics of potato tuberworm (Lepidoptera: Gelechiidae) infestation in field-stored potatoes. J Econ Entomol **98**:222-228.

Keller, S. 2003. Integrated Pest Management of the Potato Tuber Moth in Cropping Systems of Different Agroecological Zones. Margraf Publishers, Germany.

Kim, D. S., and J. H. Lee. 2003. Oviposition model of *Carposina sasakii* (Lepidoptera : Carposinidae). Ecological Modelling **162**:145-153.

Logan, J. A. 1988. Toward an Expert System for Development of Pest Simulation-Models. Environmental Entomology **17**:359-376.

Logan, J. A., and J. Powell. 2001. Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). American Entomologist **47**:160-172.

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

Logan, J. A., D. J. Wollkind, S. C. Hoyt, and L. K. Tanigoshi. 1976. Analytic Model for Description of Temperature-Dependent Rate Phenomena in Arthropods. Environmental Entomology **5**:1133-1140.

Lynch, M., and W. Gabriel. 1987. Environmental tolerance. American Naturalist **129**:283-303.

Martin, T. L., and R. B. Huey. 2008. Why "Suboptimal" is optimal: Jensen's inequality and ectotherm thermal preferences. American Naturalist **171**:E102-E118.

Mazoyer, C. 2007. Mécanismes d’interaction entre ravageurs invasifs tropicaux de la pomme de terre en Equateur. University of Montpellier, Montpellier, France.

Messenger, P. S. 1959. Bioclimatic studies with Insects. Annual Review of Entomology **4**:183-206.

Messenger, P. S., and N. E. Flitters. 1958. Effect of constant temperature environments on the egg stage of three species of hawaiian fruit flies. Annals of the Entomological Society of America **51**:109-119.

Moilanen, A. 1999. Patch occupancy models of metapopulation dynamics: Efficient parameter estimation using implicit statistical inference. Ecology **80**:1031-1043.

Moilanen, A. 2004. SPOMSIM: software for stochastic patch occupancy models of metapopulation dynamics. Ecological Modelling **179**:533-550.

Nehrbass, N., and E. Winkler. 2007. Is the Giant Hogweed still a threat? An individual-based modelling approach for local invasion dynamics of Heracleum mantegazzianum. Ecological Modelling **201**:377-384.

Nehrbass, N., E. Winkler, J. Mullerova, J. Pergl, P. Pysek, and I. Perglova. 2007. A simulation model of plant invasion: long-distance dispersal determines the pattern of spread. Biological Invasions **9**:383-395.

Neubert, M. G., and H. Caswell. 2000. Demography and dispersal: Calculation and sensitivity analysis of invasion speed for structured populations. Ecology **81**:1613-1628.

Notz, A. 1995. Influencia de la temperatura sobre la biologia de *Tecia solanivora* (Povolny) (Lepidoptera: Gelechiidae) criadas en tuberculos de papa *Solanum tuberosum* L. Boletín de Entomología Venezolana **11**:49-54.

Nwilene, F. E., K. F. Nwanze, and A. Youdeowei. 2008. Impact of integrated pest management on food and horticultural crops in Africa. Entomologia Experimentalis Et Applicata **128**:355-363.

Nyssen, J., J. Poesen, and J. Deckers. 2009. Land degradation and soil and water conservation in tropical highlands. Soil and Tillage Research **103**:197-202.

Opit, G. P., J. E. Throne, and M. E. Payton. 2010. Reproductive Parameters of the Parthenogenetic Psocid *Lepinotus reticulatus* (Psocoptera: Trogiidae) at Constant Temperatures. Environmental Entomology **39**:1004-1011.

Peairs, L. M. 1914. The Relation of Temperature to Insect Development. J Econ Entomol **7**:174-181.

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

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

Pitt, J. P. W., S. P. Worner, and A. V. Suarez. 2009. Predicting Argentine ant spread over the heterogeneous landscape using a spatially explicit stochastic model. Ecological Applications **19**:1176-1186.

Pörtner, H. O. 2002. Climate variations and the physiological basis of temperature dependent biogeography: systemic to molecular hierarchy of thermal tolerance in animals. Comparative Biochemistry and Physiology - Part A: Molecular & Integrative Physiology **132**:739-761.

Poveda, G., D. M. Alvarez, and O. A. Rueda. 2011. Hydro-climatic variability over the Andes of Colombia associated with ENSO: a review of climatic processes and their impact on one of the Earth's most important biodiversity hotspots. Climate Dynamics **36**:2233-2249.

Powsner, L. 1935. The Effects of Temperature on the Durations of the Developmental Stages of *Drosophila melanogaster*. Physiological Zoology **8**:474-520

Prasad, A., L. Iverson, M. Peters, J. Bossenbroek, S. Matthews, T. Davis Sydnor, and M. Schwartz. 2010. Modeling the invasive emerald ash borer risk of spread using a spatially explicit cellular model. Landscape Ecology **25**:353-369.

Puillandre, N., S. Dupas, O. Dangles, J. L. Zeddam, C. Capdevielle-Dulac, K. Barbin, M. Torres-Leguizamon, and J. F. Silvain. 2008. Genetic bottleneck in invasive species: the potato tuber moth adds to the list. Biological Invasions **10**:319-333.

Pumisacho, M., and S. Sherwood. 2002. El cultivo de la papa en el Ecuador. INIAP-CIP, Quito.

Radcliffe, E. B. 1982. Insect Pests of Potato. Annual Review of Entomology **27**:173-204.

Rebaudo, F., V. Crespo-Perez, J.-F. Silvain, and O. Dangles. 2011. Agent-Based Modeling of Human-Induced Spread of Invasive Species in Agricultural Landscapes: Insights from the Potato Moth in Ecuador. JASS **14**:7.

Régnière, J. 1987. Temperature-dependent deveolpment of eggs and larvae of *Choristoneura fumiferana* (Clem) (Lepidoptera, Tortricidae) and simulation of its seasonal history. Canadian Entomologist **119**:717-728.

Régnière, J. 1996. Generalized approach to landscape-wide seasonal forecasting with temperature-driven simulation models. Environmental Entomology **25**:869-881.

Régnière, J., and J. A. Logan, editors. 2003. Animal life cycle models. Kluwer Academic, Dordrecht,The Netherlands.

Régnière, J., V. Nealis, and K. Porter. 2009. Climate suitability and management of the gypsy moth invasion into Canada. Biological Invasions **11**:135-148.

Régnière, J., J. Powell, B. Bentz, and V. Nealis. submitted. Temperature Responses of Insects: Design of Experiments, Data Analysis and Modeling. Ecological Applications.

Régnière, J., and A. Sharov. 1998. Phenology of *Lymantria dispar* (Lepidoptera : Lymantriidae), male flight and the effect of moth dispersal in heterogeneous landscapes. International Journal of Biometeorology **41**:161-168.

Renault, D. 2011. Long-term after-effects of cold exposure in adult *Alphitobius diaperinus* (Tenebrionidae): the need to link survival ability with subsequent reproductive success. Ecological Entomology **36**:36-42.

Rinehart, J. P., G. D. Yocum, and D. L. Denlinger. 2000. Thermotolerance and rapid cold hardening ameliorate the negative effects of brief exposures to high or low temperatures on fecundity in the flesh fly, *Sarcophaga crassipalpis*. Physiological Entomology **25**:330-336.

Rondon, S. I. 2010. The Potato Tuberworm: A Literature Review of Its Biology, Ecology, and Control. American Journal of Potato Research **87**:149-166.

Russell, R. 1933. Insects and Climate. Geographical Review **23**:170-172.

Sakai, A. K., F. W. Allendorf, J. S. Holt, D. M. Lodge, J. Molofsky, K. A. With, S. Baughman, R. J. Cabin, J. E. Cohen, N. C. Ellstrand, D. E. McCauley, P. O'Neil, I. M. Parker, J. N. Thompson, and S. G. Weller. 2001. The population biology of invasive species. Annual Review of Ecology and Systematics **32**:305-332.

Sanderson, E. D., and L. M. Peairs. 1913. The relation of temperature to insect life. New Hampshire College of Agriculture and the Mechanic Arts, New Hampshire.

Sarmiento, F. O. 2002. Anthropogenic change in the landscapes of highland Ecuador. Geographical Review **92**:213-234.

Savage, Van M., James F. Gillooly, James H. Brown, Geoffrey B. West, and Eric L. Charnov. 2004. Effects of Body Size and Temperature on Population Growth. The American Naturalist **163**:429-441.

Schoolfield, R. M., P. J. H. Sharpe, and C. E. Magnuson. 1981. Non-Linear Regression of Biological Temperature-Dependent Rate Models Based on Absolute Reaction-Rate Theory. Journal of Theoretical Biology **88**:719-731.

Schwarz, G. 1978. Estimating dimension of a model. Annals of Statistics **6**:461-464.

Sebert-Cuvillier, E., V. Simon-Goyheneche, F. Paccaut, O. Chabrerie, O. Goubet, and G. Decocq. 2008. Spatial spread of an alien tree species in a heterogeneous forest landscape: a spatially realistic simulation model. Landscape Ecology **23**:787-801.

Shaffer, P. L., and H. J. Gold. 1985. A simulation model of population dynamics of the codling moth, *Cydia pomonella*. Ecological Modelling **30**:247-274.

Sharpe, P. J. H., and D. W. DeMichele. 1977. Reaction-kinetics of poikilotherm development. Journal of Theoretical Biology **64**:649-670.

Skarpaas, O., and K. Shea. 2007. Dispersal patterns, dispersal mechanisms, and invasion wave speeds for invasive thistles. American Naturalist **170**:421-430.

Soons, M. B., J. H. Messelink, E. Jongejans, and G. W. Heil. 2005. Habitat fragmentation reduces grassland connectivity for both short-distance and long-distance wind-dispersed forbs. Journal of Ecology **93**:1214-1225.

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

StarfieId, A. M., and A. L. Bleloch. 1986. Building models for conservation and wildlife management. Macmillan, New York.

Steigenga, M. J., and K. Fischer. 2007. Ovarian dynamics, egg size, and egg number in relation to temperature and mating status in a butterfly. Entomologia Experimentalis Et Applicata **125**:195-203.

Steigenga, M. J., and K. Fischer. 2009. Fitness consequences of variation in developmental temperature in a butterfly. Journal of Thermal Biology **34**:244-249.

Stiling, P. 2002. Ecology: Theories and Applications, 4th edition. Prentice-Hall, Inc., New Jersey.

Still, C. J., P. N. Foster, and S. H. Schneider. 1999. Simulating the effects of climate change on tropical montane cloud forests. Nature **398**:608-610.

Stillman, J. H., and G. N. Somero. 2000. A comparative analysis of the upper thermal tolerance limits of eastern Pacific porcelain crabs, genus Petrolisthes: Influences of latitude, vertical zonation, acclimation, and phylogeny. Physiological and Biochemical Zoology **73**:200-208.

Stillwell, R. C., and C. W. Fox. 2005. Complex Patterns of Phenotypic Plasticity: Interactive Effects of Temperature during Rearing and Oviposition. Ecology **86**:924-934.

Talbot, M. 1934. Distribution of ant species in the Chicago region with reference to ecological factors and physiological toleration. Ecology **15**:416-439.

Torres-Leguizamon, M., S. Dupas, D. Dardon, Y. Gomez, L. Nino, A. Carnero, A. Padilla, I. Merlin, A. Fossoud, J. L. Zeddam, X. Lery, C. Capdevielle-Dulac, O. Dangles, and J. F. Silvain. 2011. Inferring native range and invasion scenarios with mitochondrial DNA: the case of *T. solanivora* successive north-south step-wise introductions across Central and South America. Biological Invasions **13**:1505-1519.

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

Travis, J. M. J. 2010. Towards a mechanistic understanding of dispersal evolution in plants: conservation implications. Diversity and Distributions **16**:877-877.

Travis, J. M. J., C. M. Harris, K. J. Park, and J. M. Bullock. 2011. Improving prediction and management of range expansions by combining analytical and individual-based modelling approaches. Meth Ecology Evolution:Published online.

Urrutia, R. U. R., and M. Vuille. 2009. Climate change projections for the tropical Andes using a regional climate model: Temperature and precipitation simulations for the end of the 21st century. Journal of Geophysical Research-Atmospheres **114**.

Uvarov, B. P. 1931. Insects and Climate. Transactions of the Entomological Society of London **79**:1-247.

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

Vazquez, D. P., and R. D. Stevens. 2004. The latitudinal gradient in niche breadth: Concepts and evidence. American Naturalist **164**:E1-E19.

Venette, R. C., and J. R. Gould. 2006. A pest risk assessment for *Copitarsia* spp., Insects associated with importation of commodities into the United States. Euphytica **148**:165-183.

Venette, R. C., D. J. Kriticos, R. D. Magarey, F. H. Koch, R. H. A. Baker, S. P. Worner, N. N. G. Raboteaux, D. W. McKenney, E. J. Dobesberger, D. Yemshanov, P. J. De Barro,

W. D. Hutchison, G. Fowler, T. M. Kalaris, and J. Pedlar. 2010. Pest Risk Maps for Invasive Alien Species: A Roadmap for Improvement. Bioscience **60**:349-362.

Vinatier, F., F. Lescourret, P. F. Duyck, O. Martin, R. Senoussi, and P. Tixier. 2011. Should I Stay or Should I Go? A Habitat-Dependent Dispersal Kernel Improves Prediction of Movement. Plos One **6**.

Vinatier, F., P. Tixier, C. Le Page, P. F. Duyck, and F. Lescourret. 2009. COSMOS, a spatially explicit model to simulate the epidemiology of *Cosmopolites sordidus* in banana fields. Ecological Modelling **220**:2244-2254.

Wagner, T. L., H.-I. Wu, P. J. H. Sharpe, R. M. Schoolfield, and R. N. Coulson. 1984. Modeling Insect Development Rates: A Literature Review and Application of a Biophysical Model. Annals of the Entomological Society of America **77**:208-225.

Wagner, T. L., H. I. Wu, R. M. Feldman, P. J. H. Sharpe, and R. N. Coulson. 1985. Multiple-cohort approach for simulating development of insect populations under variable temperatures. Annals of the Entomological Society of America **78**:691-704.

Walters, R. J., and M. Hassall. 2006. The temperature-size rule in ectotherms: May a general explanation exist after all? American Naturalist **167**:510-523.

Wang, J. Y. 1960. A critique of the heat unit approach to plant-response studies. Ecology **41**:785-790.

Williams, J. J., W. D. Gosling, A. L. Coe, S. J. Brooks, and P. Gulliver. 2011. Four thousand years of environmental change and human activity in the Cochabamba Basin, Bolivia. Quaternary Research **76**:58-68.

Willis, J. C., D. A. Bohan, Y. H. Choi, K. F. Conrad, and M. A. Semenov. 2006. Use of an individual-based model to forecast the effect of climate change on the dynamics, abundance and geographical range of the pest slug *Deroceras reticulatum* in the UK. Global Change Biology **12**:1643-1657.

Worner, S. P. 1991. Use of Models in Applied Entomology: The Need for Perspective. Environmental Entomology **20**:768-773.

Worner, S. P. 1992. Performance of phenological models under variable temperature regimes - Consequences of the Kaufmann or rate summation effect. Environmental Entomology **21**:689-699.

Young, K., and J. Lipton. 2006. Adaptive Governance and Climate Change in the Tropical Highlands of Western South America. Climatic Change **78**:63-102.

Young, K. R. 1997. Wildlife conservation in the cultural landscapes of the central Andes. Landscape and Urban Planning **38**:137-147.

Young, K. R. 2009. Andean land use and biodiversity: Humanized ladscapes in a time of change. Annals of the Missouri Botanical Garden **96**:492-507.

Zahiri, B., Y. Fathipour, M. Khanjani, S. Moharramipour, and M. P. Zalucki. 2010. Preimaginal Development Response to Constant Temperatures in Hypera postica (Coleoptera: Curculionidae) : Picking the Best Model. Environmental Entomology **39**:177-189.

GENERAL APPENDICES

APPENDIX S10

Journal of Applied Ecology

Journal of Applied Ecology 2009, **46**, 1115–1121 doi: 10.1111/j.1365-2664.2009.01703.x

Crop damage increases with pest species diversity: evidence from potato tuber moths in the tropical Andes

Olivier Dangles*[,1,2], **Verónica Mesías**[1], **Verónica Crespo-Perez**[1] **and Jean-François Silvain**[2]

[1]*PUCE, Facultad de Ciencias Exactas y Naturales, Quito, Ecuador; and* [2]*IRD, UR 072, UPR 9034, CNRS, LEGS, Gif-sur Yvette Cedex, France and Université Paris-Sud 11, Orsay, France*

Summary

1. Insect pests in agricultural systems are one of the major causes of damage to crop production and storage worldwide. However, the study of the effect of multiple pests on agricultural productivity has remained largely disconnected from the ongoing debate on how species diversity affects the productivity of ecosystems. The aim of our study is to use information from crop studies to inform the debate on species diversity and ecosystem productivity.

2. We present the results of an experimental study that manipulated the species richness of three tuber feeding moth species (Lepidoptera: Gelechiidae) at constant larval density. We measured the influence of this manipulation on (1) damage to the economically most important crop in the Andean region, the potato *Solanum tuberosum* and (2) the performance of the moths as a consequence of feeding rates.

3. Our results showed that the three pest species together cause more damage to the crop than is predicted from the effects of each pest alone. This resulted in significant increases in pupal biomass and fecundity.

4. Potential mechanisms to explain our results are (1) more complete resource utilization and thus greater crop damage (feeding complementarity) and (2) negative interactions, where intra-specific interactions are greater than inter-specific interactions.

5. *Synthesis and applications.* Our findings may have important consequences for integrated pest management in poor tropical countries. Biodiversity in many tropical countries is decreasing rapidly, leading to reductions in ecosystem services such as biocontrol and pollination. At the same time an increasing number of species, many of them agricultural pests, are being introduced by humans. Our results show that the potential complementarity effects among pest species may increase damage to field crops to a larger extent than previously expected. Control strategies to limit the introduction of new pest species are therefore urgently needed in these countries where the daily management of biological resources is largely in the hands of poor rural people and local government staff with limited funding.

Key-words: additive effects, biocontrol, biodiversity–ecosystem function relationship, complementarity, crop damage, fitness, potato moths

Introduction

Insect pests in agricultural systems are one of the major causes of damage to crop production and storage (Thomas 1999). In tropical countries, these pests are believed to cause losses approaching 60–70%, principally in stored products (Thomas 1999 and references therein; Nwilene, Nwanze & Youdeowei 2008). Agriculture has long faced a considerable challenge from managing several pest species on a single crop. This has resulted in the development of multi-pest research and survey programmes and specific integrated pest management strategies (e.g. Johnson 1990; Willocquet *et al.* 2008). Surprisingly, the study of the effects of multiple pests on agricultural produc-

---

*Correspondence author. E-mail: dangles@legs.cnrs-gif.fr tivity has remained largely disconnected from the ongoing debate on how species diversity affects the functioning of ecosystems. Whereas the former line of research has focused mostly on the effect of non-additive species interactions in crop consumption (Castella, Dollona & Savary 2005; Davidson, Peairs & Khosla 2007), the latter has concentrated on additive mechanisms, independently of overall abundance, by which species diversity influences resource consumption, with emphasis on terrestrial plant communities (Loreau & Hector 2001; Hooper *et al.* 2005; Callaway 2007). Both additive and non-additive insect species interactions probably have an impact on plant damage (Kaplan & Denno 2007), but, so far, insights from studies of the diversity–function debate have rarely been applied to understanding the functional significance of herbivore insect diversity in agricultural systems (Hammons *et al.* 2009).

There are several practical and conceptual reasons for being concerned with insect pest species interactions in agricultural systems. First, since the establishment of agriculture, planted and stored crops have always been infested by multiple pest species (Savary *et al.* 1994). This is still the rule today for many economically important crops over the world such as rice *Oryza sativa* L. in Asia (Savary *et al.* 1994), corn *Zea mays* L. and sorghum *Sorghum bicolor* L. Moench in Africa (Le Rü *et al.* 2006), wheat *Triticum aestivum* L. in Europe (Daamen & Stol 1994), corn *Z. mays* in North America (Davidson *et al.* 2007) and potato *Solanum tuberosum* L. in South America (Dangles *et al.* 2008). Secondly, the increased transport of species by humans in recent years has substantially increased the diversity of many local pest communities in agricultural and forest systems (Duyck *et al.* 2006; Dangles *et al.* 2008; Preisser *et al.* 2008). Because many of these new pests are invasive, often free of natural enemies (Colautti *et al.* 2004) and able to reach high densities (e.g. Paine 2008), the likelihood and potential importance of inter-specific interactions have increased (e.g. Duyck *et al.* 2006). Thirdly, research on biodiversity and ecosystem functions in managed ecosystems, such as agricultural landscapes, has focused on the effects of biodiversity loss on ecosystem functions and services (e.g. crop variety: Vandermeer *et al.* 2002; Li *et al.* 2007; natural enemy diversity, Wilby & Thomas 2002; Cardinale *et al.* 2003; pollinator diversity, Morris 2003; Kremen *et al.* 2007). Much less information is available on the functional consequences of the increase in the diversity of some specific groups of organisms that negatively impact ecosystem productivity (but see Simberloff 2006; Bulleri, Bruno & Benedetti-Cecchi 2008).

Here, we present the results of an experimental study that manipulated the species richness of three tuber feeding moth species *Phthorimaea operculella* Zeller, *Tecia solanivora* Povolny and *Symmetrischema tangolias* Gyen (Lepidoptera: Gelechiidae), one of the most damaging crop pest complexes in the Northern Andes. We measured the influence of this manipulation on (1) damage to the economically most important crop in the Andean region, the potato *S. tuberosum* and on (2) performance of these three moth species (in terms of survival, biomass and fecundity) as a consequence of resource utilization. Our study was motivated by two observations. First, within the last 30 years, these three moth species have been brought together in combinations of two or three species into potato fields of the Northern Andes (Venezuela, Colombia, Ecuador, Peru and Bolivia) through successive introductions from different origins in South and Central America (Dangles *et al.* 2008). Although taxonomically related, these species are significantly different in body size, life history, autecology and pathogen resistance (see Dangles *et al.* 2008) which may result in functional differences in their resource utilization and crop damage. Secondly, in the study region, both storage shelters and sacks of potatoes are now commonly infested with different mixtures of the three moth species. However, depending on latitude and altitude, there are strong differences in crop damage observed among regions. Despite the wide number of natural and anthropogenic variables influencing crop damage in the field (Castillo 2005), data from 31 Ecuadorian potato fields suggest higher crop damage rates at sites where two or three moth species are present than at sites where there is only one species (see Fig. 1 and its legend for details). These observations led us to hypothesize that moth species richness may play a role in the damage these pests cause to potato crops, which mainly occurs under storage conditions in Ecuador. The results of our study indicate that the three pest species together increase damage to

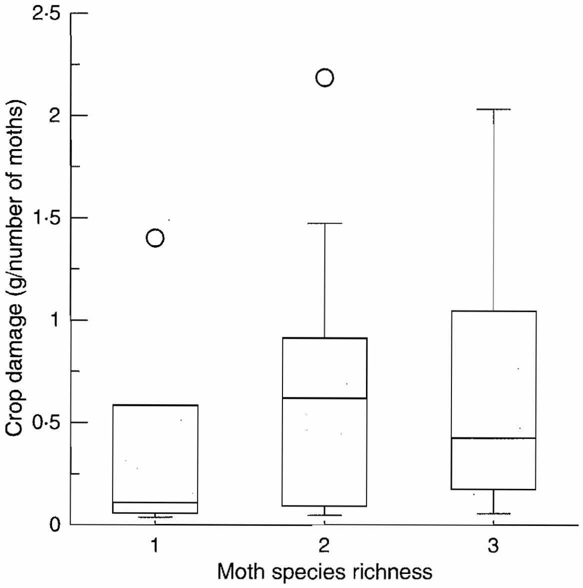


Fig. 1. Box-whisker plot of the intensity of damage in potato fields at sites with different richness of the three potato tuber moth species in Ecuador (*Tecia solanivora*, *Symmetrischema tangolias*, *Phthorimaea operculella*). The endpoints of both whiskers indicate minimum and maximum values. Circles indicate which observations can be considered outliers. Data are from 31 potato field sites (n = 8, 13 and 10 for the one-, two- and three-species groups respectively) surveyed in the Central Ecuadorian Andes (for details on the study region see Dangles *et al.* 2008). Crop damage was measured at harvest. It is expressed as the biomass of damaged tubers in five randomly selected plants in the potato field divided by the total number of adult potato tuber moths of the three species collected with pheromone traps during the 3 months preceding harvest date (for more details on methods see Dangles *et al.* 2008).

the crop to a greater extent than is predicted from the added effects of each pest considered separately, with significant consequences for their performance. Our study further revealed that both pupal biomass and female fecundity of the three species were higher in the multispecies treatments than in single-species treatments.

Materials and methods

EXPERIMENTAL DESIGN

We performed an experiment investigating the effect of manipulated species richness, from one to three moth species, on potato damage. Experiments were conducted under controlled conditions (i.e. in a room with 70 ± 10% relative humidity, 17 ± 1·5 °C and LD 12 : 12 period). The mean temperature of the room corresponded to mean temperatures in storage structures at sites where the three species co-occur (see Dangles *et al.* 2008). Our controlled experimental design consisted of eight treatments replicated 10 times; three single-species treatments with 12 individuals of *T. solanivora*, *S. tangolias* and *S. personatum*, three two-species treatments (6 + 6 individuals) with *T. solanivora* and *S. tangolias*, *T. solanivora* and *P. operculella*, *S. tangolias*, and *P. operculella*; one three-species treatment (4 + 4 + 4 individuals) with *T. solanivora* and *P. operculella* and *S. tangolias*, and one control treatment to provide information on tuber-mass loss in the absence of larvae. The constant total density of 12 individuals in each treatment allowed us to test for the effect of diversity without density effects (see Jonsson & Malmqvist 2000). This density was representative of that found in infested sacks (range: 8–18 larvae after 20 days of tuber storage, Dangles and Carpio, unpublished data). For each treatment, potato tubers [*S. tuberosum* L., v. *Leona blanca* (Solanaceae) which is equally accepted by the three species] of similar size (31·6 ± 6·9 g) were weighed to the nearest 0·1 mg (Balance TU-OI, FA-2104, Mhand, Fuzhou, China) and placed individually in a 250-mL plastic container covered with nylon mesh. Depending on the number of larvae in each treatment, tubers were inoculated with the corresponding number of eggs taken from permanent cultures in our laboratory. Laboratory colonies were replaced every 3 months with hundreds of larvae collected in two to three potato sacks from the Salcedo market (Salcedo, Cotopaxi Province, Ecuador). Eggs were all of the same age, i.e. laid within 24 hours preceding the experiment. Egg mortality was checked every day using a stereomicroscope (LEICA, MZ3, Leica Microsystems, Wetzlar, Germany). After pupation, tubers were dissected to assess larval mortality and tubers were weighed to the nearest 0·1 mg. Data on loss of tuber mass were corrected for loss caused by factors other than larva consumption (primarily evapotranspiration) as assessed in the larva-free controls. Correction for the effects of moth mortality on potato consumption was made by assuming that dead individuals had lived for half the experimental time. Further, the mass of consumed potato per unit pupal mass was used in the analyses to account for among species differences in biomass.

In addition to larva mortality, we measured pupae biomass (to the nearest 0·1 mg) and the fecundity of emerging females in each treatment as proxies for moth performance. Fecundity was measured as total number of eggs laid per female. Pairs of adult moths were placed in cylindrical plastic containers (h = 20 cm, Ø = 15 cm) covered with mesh nylon (1 mm). Dilute sugar solution provided food and water through cotton swabs. In all three species, the sex ratio was *c.* 1 : 1 whatever the population density. Oviposition generally started 1 day after adult emergence and the majority of eggs were laid within the first 4 days following mating. For each replicate of each treatment, the fecundity (number of eggs laid by female) of all emerged adult pairs was recorded daily (for additional life table data on the three species, see Dangles *et al.* 2008). All adults lived for > 6 days.

DATA ANALYSES

The experiment was a nested design with each species identity treatment nested within a species richness treatment (Jonsson & Malmqvist 2000). This design allowed us to separate the effects of species richness and species identity using nested analysis of variance (ANOVA), including all species combinations in each species richness treatment. We further compared the individual effects on loss of tuber mass caused by each of the three moth species in a one-way ANOVA on log-transformed data. Average values of tuber mass loss in the single-species experiments were then used to predict the results in the multispecies treatments; the residuals from comparisons between predicted and observed mass losses were subsequently used in a second nested ANOVA using data from the experiments with two and three species only (Jonsson *et al.* 2002).

Following Loreau & Hector (2001), we measured the net effect of species richness on three performance variables of moths, larva survival (ΔF1), pupa biomass (ΔF2) and female fecundity (ΔF3), by the difference between the observed values in the mixture treatments *j* and their expected values under the null hypothesis that there is no additive effect, as follows:

$$\Delta F = \sum_i F_{Oj} - \sum_i F_{Ej}$$

where F_{Oj} and F_{Ej} are the observed and expected performance values of species *i* in the mixture treatment *j* respectively. The influence of species richness and composition on the three performance variables was further analysed with a nested ANOVA. All analyses were performed using R 2.8.1 (http://cran.r-project.org/).

Results

Mean loss of tuber mass in the control treatment was 1·91 g (SD = ±0·29), about 6·0% of the initial biomass, suggesting a good conservation of tuber quality during the experiment (see Cargill, Briik & Forbush 1989). Taking animal biomass into account, we found significant differences in the feeding rate of the three species in the one-species treatments (Fig. 2). On average, *S. tangolias* had the greatest impact on loss of tuber mass, followed by *T. solanivora* and *P. operculella* (one-way ANOVA, d.f. = 2, F = 8·2351, P = 0·0016). Loss of potato tuber mass was significantly affected by moth species richness and identity (nested ANOVA; Table 1, Fig. 2). When species were mixed, loss of tuber mass increased significantly with the number of moth species following an exponential decay model (see Fig. 2, R^2 = 0·982, F_{stat} = 676·63, Spearman test, P < 0·001). Tuber mass loss was significantly greater in three-species treatments compared with two-species treatments (nested ANOVA, Table 2) when controlling for differences in single species efficiency.

We found no significant net effect of diversity on larval survival (Fig. 3a, nested ANOVA, Table 3). In mixture treatments, larval survival was similar among species (one-way ANOVA, d.f. = 8, F = 1·424, P = 0·199). In contrast, we found a significant positive net effect of species richness on both pupal

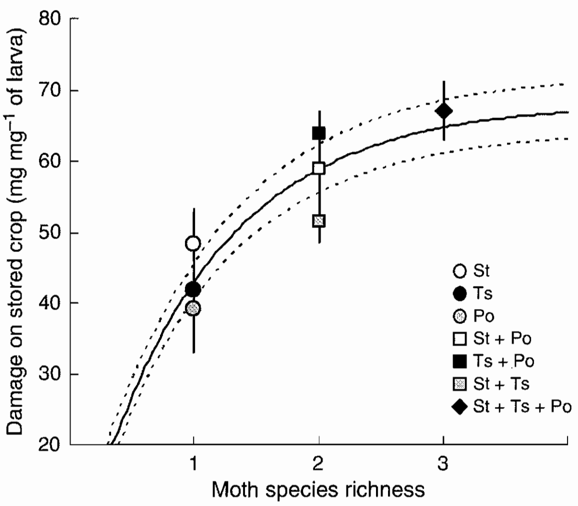


Fig. 2. Pest species richness (potato tuber moth larvae) vs. damage on stored potato tuber biomass. Larval density in each treatment was constant (n = 12). Tuber damage values were normalized by larval biomass (mg tuber/mg larva) to account for differences in species size. Error bars represent ± 1 SD with 10 replicates. Data were adjusted with an exponential decay model (increasing form) as follows: $y = a + b \times \exp^{-x}$ with $a = 68.03$, $b = -68.06$, $R^2 = 0.985$, $F_{\mathrm{stat}} = 676.63$, $P < 0.001$ (Spearman test) revealing a significant positive effect of pest diversity on crop biomass. Dashed lines represent 95% confidence intervals. St = *S. tangolias*, Po = *P. operculella*, Ts = *T. solanivora*.

Table 1. Nested ANOVA for tuber consumption, including all moth species identity treatments

Source	d.f.	Sum of Squares	Mean of squares	*F*	*P*
Species number	2	2320·6	1160·3	58·99	<0·001
Species combination	4	3807·0	951·8	48·39	<0·001
Residuals	63	1239·1	19·7		

Table 2. Nested ANOVA of the effects of number of species (two or three) and species combination on residual tuber mass loss (mg per mg of larva)

Source	d.f.	Sum of Squares	Mean of squares	*F*	*P*
Species number	1	187·01	187·01	13·50	0·0008
Species combination	2	77·07	38·53	2·78	0·0753
Residuals	36	498·89	13·86		

biomass and female fecundity (Fig. 3b, c). For both variables, the net diversity effect was significantly greater in the three-species treatment than in the two-species treatments (nested ANOVA, Table 3), although the difference was much greater for pupal biomass than for female fecundity. In general, the effect of species richness was more variable for fecundity than for larval survival and pupal biomass, especially in the three-species treatment where the number of potential adult pairs for each treatment was only two.

Discussion

FROM SMALL-SCALE EXPERIMENTS TO FIELD CONDITIONS

Our results suggest that pest species richness can increase damage to crops. However, although laboratory experiments are helpful for understanding the functional role of diversity among competing species, the more complicated impact of diversity on natural (agro)ecosystem productivity is often not entirely predictable from such small-scale experiments (Loreau, Naeem & Inchausti 2002). The complexity of natural systems includes confounding factors such as community evenness (Dangles & Malmqvist 2004), dispersal (France & Duffy 2006) or trophic interactions (Duffy *et al.* 2007) that are likely to complicate predictions derived from experimental studies. Even though we addressed the question of the effect of pest species richness on crop damage in a small-scale manipulation experiment, we consider that our findings are likely to be, to some extent, valid also under field conditions. It is unlikely that additional trophic levels may qualitatively change diversity effects observed in our experiments because the three moth species have virtually no predators/parasites when they feed inside the tuber and very few (mainly poultry and insectivorous birds) when they pupate and emerge (Castillo 2005). Moreover, a heap of potatoes stored in traditional storage structures in the Andes is not strikingly different from our experimental units; indeed, once recently hatched larvae have entered the tuber they will develop there until they pupate (Dangles *et al.* 2008). However, we acknowledge that avoidance mechanisms of pre-infested tubers by young larvae or by ovipositing females (currently being investigated by our team) may modify the frequency of co-occurrence of couples of species in the same tuber (see Choh, Uefune & Takabayashi 2008). Another limitation in our experimental design was that we kept constant both the proportion of each moth species and the total larval densities in all diversity treatments (substitutive design). Several studies have shown, however, that evenness of interacting organisms can influence resource use (Dangles & Malmqvist 2004) and that the effects of species richness on function can be density dependent (Griffiths *et al.* 2008). Although in our case the natural range of larval abundances inside the potato is strongly limited by tuber size (therefore limiting abundance gradient effects), further studies on how potato moth species assemble under both field and storage conditions would be necessary to predict diversity effects more accurately.

IMPACT OF SPECIES RICHNESS ON CROP DAMAGE

Our study documents a case of synergetic interaction within a complex of tuber feeding moth species. We found that when all three moth species were together, the damage to potato tubers was higher than predicted from the summed impact of each species alone. These results confirm previous experimental studies that have shown the importance of animal consumer diversity on resource consumption (Duffy *et al.* 2001; Jonsson *et al.* 2002; Matthiessen *et al.* 2007). Individual species effects

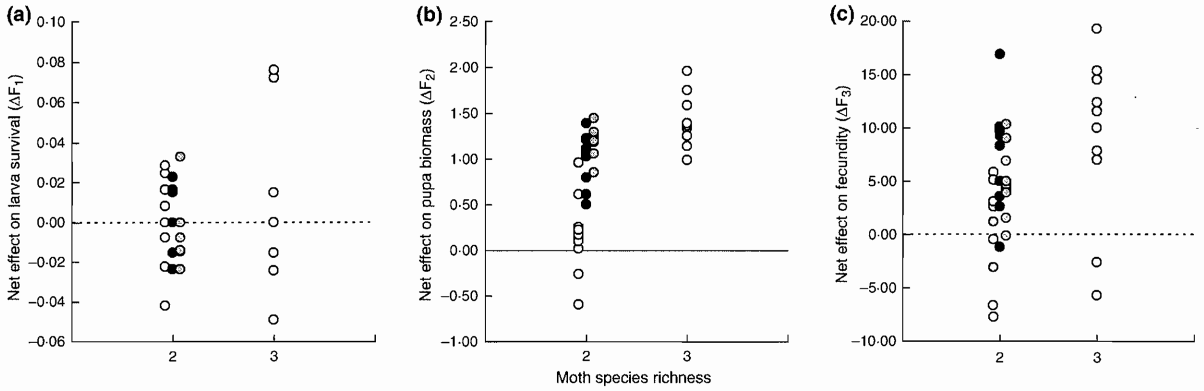


Fig. 3. Net effect of species richness on three performance variables of potato tuber moths: (a) larva survival, (b) pupa biomass, (c) female fecundity. Each plot represents one of 10 replicates. For clarity in the data representation, the three two-species treatments are slightly offset from each other in the figure. Open dots: *T. solanivora* + *S. tangolias*, Black dots: *S. tangolias* + *P. operculella*; Grey dots: *T. solanivora* + *P. operculella*.

Table 3. Nested ANOVA of the net effect of number of species (two or three) and species combination on larval survival, pupal biomass and female fecundity

Source	d.f.	Sum of squares	Mean of squares	*F*	*P*
(a) Larva survival					
Species number	1	0·00036	0·00037	0·486	0·4902
Species combination	2	0·00319	0·00159	2·109	0·1361
Residuals	36	0·02722	0·00075		
(b) Pupa biomass					
Species number	1	2·8861	2·8861	31·267	< 0·0001
Species combination	2	5·9833	2·9916	32·410	< 0·0001
Residuals	36	3·3230	0·0923		
(c) Female fecundity					
Species number	1	167·74	167·74	5·6549	0·0228
Species combination	2	265·52	132·76	4·4757	0·01837
Residuals	34	1067·84	29·66		

in this study are different from the situation where a single species has exceptionally large effects on process rates (i.e. the 'sampling effect'; Huston 1997), as all species were included in each species richness treatment. Instead, certain combinations of species had greater effects on tuber consumption, especially in multispecies treatments where *P. operculella* was included (Figs 2 and 3), revealing a significant effect of species identity in addition to a species richness effect.

Several mechanisms, such as niche partitioning (Finke & Snyder 2008) and facilitation (Cardinale, Palmer & Collins 2002; Bulleri *et al.* 2008) have been shown to contribute to increases in ecosystem functioning/production with diversity. In our case, direct observation of the interior of the tubers at the end of the experiment revealed that the three species exploited tuber resources in different ways. The smallest species, *P. operculella*, appeared to feed on the periphery of tubers, whereas the two larger species, *T. solanivora* and *S. tangolias*, both burrowed deep tunnels into the centre of the tubers. Such differences in the spatial distribution of feeding larvae suggest two mechanisms that can explain our results. (1) It allows more complete resource utilization by the larvae and thus greater damage consistent with a case of 'feeding complementarity' already reported in aquatic shredding invertebrates (Jonsson *et al.* 2002), invertebrate predators in crops (Snyder *et al.* 2006) and herbivorous coral fish (Burkepile & Hay 2008). (2) It can produce more intense intra-specific interactions that would hamper process rates more in species-poor situations compared to where encounters and interactions take place primarily between species (Jonsson & Malmqvist 2000). As predicted by Loreau & Hector (2001), niche complementarity of the three species would potentially enhance the rate of tuber loss beyond that of the best performing single species, which was verified in our experiment. Here, again it is important to record that, assuming constant resource availability, mechanisms driving species richness effects might vary depending on both relative and total species abundance in the assemblage (Griffiths *et al.* 2008).

Our study further revealed that both pupal biomass and female fecundity of the three species were higher in the multi-species treatments than in single-species treatments. Individual performance (e.g. survival and fecundity) has been shown to be influenced by inter-specific interactions in plant (Callaway 2007; Lortie & Turkington 2008) and animal communities (e.g. Kaplan & Denno 2007 for insects). However, much less is known about the effect of species richness on individual performance in multi-species animal communities, and our study is one of the few manipulative experiments that addresses this issue (see also Snyder *et al.* 2006 for invertebrate predators). In our experiment, the increase in resource consumption and/or lower intra-specific crowding density of larvae in multi-species treatments may have led to the observed increased pupal biomass and female reproductive performance (Danthanarayana, Hamilton & Khoul 1982; Zheng *et al.* 1993). These results suggest that pest species diversity has a significant effect not only on crop damage level but also on pest population dynamics in locations where two or three species coexist. Further studies on the performance properties of insect pest populations in complex mixtures of co-occurring species will provide insights not only in our understanding of pest population dynamics but also in the contribution of indirect interactions to the organization of phytophagous insect communities (Kaplan & Denno 2007).

SYNTHESIS AND APPLICATIONS

Although crops are almost universally subject to attack by multiple herbivores and pathogens, our understanding of how multiple plant enemies affect each other's dynamics and damage on plants has not been considered in detail by crop scientists (see Fournier *et al.* 2006). In this context, the results of this study have two major implications for applied ecologists studying crop management and biological control. First, our results indicate that complementarity effects among herbivores species may increase damage to field crops to a larger extent than previously expected. This finding is of particular concern for poor tropical countries where biodiversity is decreasing rapidly (therefore decreasing ecosystems services such as biocontrol and pollination), while at the same time an increasing number of species (many of them agricultural pests) are introduced by humans at accelerating rates (Mooney & Hobbs 2000). Moreover, the generally warm and/or diverse climatic conditions in tropical countries may favour the population dynamics of introduced pests (see Dangles *et al.* 2008), which itself can be fostered by positive interactions among species. Instead of focusing on one particular pest species, potato growers should therefore aim to limit the diversity of potato moths by using non-specific management strategies. Because the three pest species have different flight phenologies and attack behaviour in the field (Roux 1993; Castillo 2005), farmers should concentrate their efforts at the storage stage. They could for example use control strategies that physically protect tubers against larva attack, whatever the species (see Pollet, Barragan & Iturralde 2004). At a regional level, reinforced control strategies to limit the introduction of new herbivorous pest species are urgently needed in developing countries where the daily management of biological resources is largely in the hands of poor rural people and local government staff with little operational funding.

Secondly, the evidence of complementary interactions among multiple agents on crops has promising applications in biological control terms, as previously reported for the multiple enemy effects on pest suppression (Cardinale *et al.* 2003; Snyder *et al.* 2006). In the specific case of herbivores, our results provide interesting insights in the context of weed control. Although a number of studies have shown that a single species of herbivorous insect can result in a significant reduction of weed biomass (Zwolfer & Harris 1971; Oraze & Grigarick 1992; Sheldon & Creed 1995) our findings indicate that the impact of multiple herbivores can be higher. If the aim of weed management programmes is to maximize the overall impact of herbivory on target plant populations, then combinations of herbivores (or in a broader sense, of agents) exploiting a similar host and interacting synergistically will be especially valuable (see Denoth, Frid & Myers 2002; Davis *et al.* 2006; Fournier *et al.* 2006). Moreover, while the present work focused on additive effects within one trophic level, further studies should examine the effects of species diversity effect across trophic levels (see for example Hämback, Agren & Ericsson 2000). This lies at the heart of the present diversity–ecosystem function debate and is likely to have important applications for crop management, especially in poor tropical countries that strongly depend on agricultural resources.

Acknowledgements

This work was part of the research conducted within the project "Biopesticide development and diffusion for the control of potato moths" (C14-026) funded by the McKnight Foundation. Additional funding was provided by the School of Biology of the Catholic Pontifical University of Ecuador. The authors are grateful to J. Padilla, C. Mazoyer and P. Rosero for technical assistance during the experiment. We are grateful to F. Anthelme, J. Casas, S. Dupas, M. Jonsson and B. LeRü for constructive criticisms and to C. Keil for the linguistic revision of the manuscript. The authors are grateful to the editor and two anonymous reviewers for their helpful comments on a previous version of the manuscript.

References

Bulleri, F., Bruno, J.F. & Benedetti-Cecchi, L. (2008) Beyond competition: incorporating positive interactions between species to predict ecosystem invasibility. *Plos Biology*, **6**, e162.

Burkepile, D.E. & Hay, M.E. (2008) Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. *Proceedings of the National Academy of Sciences of the USA*, **105**, 16201–16206.

Callaway, R.M. (2007) *Positive Interactions and Interdependence in Plant Communities*. Springer, The Netherlands.

Cardinale, B.J., Palmer, M.A. & Collins, S.L. (2002) Species diversity increases ecosystem functioning through interspecific facilitation. *Nature*, **415**, 426–429.

Cardinale, B.J., Harvey, C.T., Gross, K. & Ives, A.R. (2003) Biodiversity and biocontrol: emergent impacts of a multi-enemy assemblage on pest suppression and crop yield in an agroecosystem. *Ecology Letters*, **6**, 857–865.

Cargill, B.F., Briik, R.C. & Forbush, T.D. (1989) *Potato Storage: Technology and Practice*, Proceedings of the American Society of Agriculture, 332 p.

Castella, J.C., Dollona, K. & Savary, S. (2005) Path coefficient analysis to assess yield losses due to a multiple pest complex in cotton in Thailand. *International Journal of Tropical Insect Science*, **25**, 39–49.

Castillo, G.M. (2005) *Determinacion del Ciclo de Vida de las Polillas de la Papa* Symmetrischema tangolias *(Gyen) y Tecia solanivora (Povolny) Bajo Condiciones Controladas de Laboratorio*. Dissertation. Central University of Ecuador, Quito, Ecuador.

Choh, Y., Uefune, M. & Takabayashi, J. (2008) Diamondback moth females oviposit more on plants infested by non-parasitised than by parasitized conspecifics. *Ecological Entomology*, **33**, 565–568.

Colautti, R.I., Ricciardi, A., Grigorovich, I.A. & MacIsaac, H.J. (2004) Is invasion success explained by enemy release hypothesis? *Ecology Letters*, **7**, 721–733.

Daamen, R.A. & Stol, W. (1994) Surveys of cereal diseases and pests in the Netherlands. 6. Occurrence of insect pests in winter wheat. *Netherland Journal of Plant Pathology*, **99**, 51–56.

Dangles, O. & Malmqvist, B. (2004) Species richness-decomposition relationships depend on species dominance. *Ecology Letters*, **7**, 395–402.

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

Danthanarayana, W., Hamilton, J.G. & Khoul, S.P. (1982) Low density larval crowding in the light brown apple moth, *Epiphyas postvittana* and its ecological significance. *Entomologia Experimentalis et Applicata*, **31**, 352–358.

Davidson, S.A., Peairs, F.B. & Khosla, R. (2007) Insect pest densities across site-specific management zones of irrigated corn in Northeastern Colorado. *Journal of Economical Entomology*, **100**, 781–789.

Davis, A.S., Landis, D.A., Nuzzo, V., Blossey, B., Gerber, E. & Hinz, H.L. (2006) Demographic models inform selection of biocontrol agents for garlic mustard (*Alliaria petiolata*). *Ecological Applications*, **16**, 2399–2410.

Denoth, M., Frid, L. & Myers, J.H. (2002) Multiple agents in biological control: improving the odds? *Biological Control*, **24**, 20–30.

Duffy, J.E., MacDonald, K.S., Rhode, J.M. & Parker, J.D. (2001) Grazer diversity, functional redundancy, and productivity in seagrass beds: an experimental test. *Ecology*, **82**, 2417–2434.

Duffy, J.E., Cardinale, B.J., France, K.E., McIntyre, P.B., Thébault, E. & Loreau, M. (2007) The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters*, **10**, 522–538.

Duyck, P.-F., David, P., Junod, G., Brunel, C., Dupont, R. & Quilici, S. (2006) Importance of competition mechanisms in successive invasions by polyphagous tephritids in La Réunion. *Ecology*, **87**, 1770–1780.

Finke, D.L. & Snyder, W.E. (2008) Niche partitioning increases resource exploitation by diverse communities. *Science*, **321**, 1488–1490.

Fournier, V., Rosenheim, J.A., Brodeur, J., Diez, J.M. & Johnson, M.W. (2006) Multiple plant exploiters on a shared host: testing for nonadditive effects on plant performance. *Ecological Applications*, **16**, 2382–2398.

France, K.E. & Duffy, J.E. (2006) Diversity and dispersal interactively affect predictability of ecosystem function. *Nature*, **441**, 1139–1143.

Griffiths, G.J.K., Wilby, A., Crawley, M.J. & Thomas, M.B. (2008) Density-dependent effects of predator species richness in diversity–function studies. *Ecology*, **89**, 2986–2993.

Hämback, P.A., Agren, J. & Ericsson, L. (2000) Associational resistance: insect damage to purple loosestrife reduced in thickets of sweet gale. *Ecology*, **81**, 1784–1794.

Hammons, D.L., Kurtural, S.K., Newman, M.C. & Pottera, D.A. (2009) Invasive Japanese beetles facilitate aggregation and injury by a native scarab pest of ripening fruits. *Proceedings of the National Academy of Sciences of the USA*, **106**, 3686–3691.

Hooper, D.U., Chapin III, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J. & Wardle, D.A. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 3–35.

Huston, M.A. (1997) Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia*, **110**, 449–460.

Johnson, K.B. (1990) Assessing multiple pest populations and their effects on crop yield. *Crop Loss Assessment in Rice* (ed. P.S. Teng), pp. 203–213. IRRI. Los Baños, Philippines.

Jonsson, M. & Malmqvist, B. (2000) Ecosystem process rate increases with animal species richness: evidence from leaf-eating, aquatic insects. *Oikos*, **89**, 519–523.

Jonsson, M., Dangles, O., Malmqvist, B. & Guerold, F. (2002) Simulating species loss following disturbance: assessing the effects on process rates. *Proceedings of the Royal Society of London B*, **269**, 1047–1052.

Kaplan, I. & Denno, R.F. (2007) Interspecific interactions in phytophagous insects revisited: a quantitative assessment of competition theory. *Ecology Letters*, **10**, 977–994.

Kremen, C., Williams, N.M., Aizen, M.A., Gemmill-Herren, B., Le Buhn, G., Minckley, R., Packer, L., Potts, S.G., Roulston, T., Steffan-Dewenter, I., Vázquez, D.P., Winfree, R., Adams, L., Crone, E.E., Greenleaf, S.S., Keitt, T.H., Klein, A.M., Regetz, J. & Ricketts, T. (2007) Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land use change. *Ecology Letters*, **10**, 299–314.

Le Rü, B.P., Ong'amo, G.O., Moyal, P., Ngala, L., Musyoka, B., Abdullah, Z., Cugala, D., Defabachew, B., Haile, T.A., Kauma Matama, T., Lada, V.Y., Negassi, B., Pallangyo, K., Ravolonandrianina, J., Sidumo, A., Omwega, C.O., Schulthess, F., Calatayud, P.A. & Silvain, J.F. (2006) Diversity of lepidopteran stem borers on monocotyledonous plants in eastern Africa and the islands of Madagascar and Zanzibar revisited. *Bulletin of Entomological Research*, **96**, 555–563.

Li, L., Li, S.-M., Sun, J.-H., Zhou, L.-L., Bao, X.-G., Zhang, H.-G. & Zhang, F.-S. (2007) Diversity enhances agricultural productivity via rhizosphere phosphorus facilitation on phosphorus-deficient soils. *Proceedings of the National Academy of Sciences of the USA*, **104**, 11192–11196.

Loreau, M. & Hector, A. (2001) Partitioning selection and complementarity in biodiversity experiments. *Nature*, **412**, 72–76.

Loreau, M., Naeem, S. & Inchausti, P. (2002) Perspectives and challenges. *Biodiversity and Ecosystem Functioning: Synthesis and Perspective* (eds M. Loreau, S. Naeem & P. Inchausti), pp. 237–242. Oxford University Press, Oxford.

Lortie, C.J. & Turkington, R. (2008) Species-specific positive effects in an annual plant community. *Oikos*, **117**, 1511–1521.

Matthiessen, B., Gamfeldt, L., Jonsson, P.R. & Hillebrand, H. (2007) Effects of grazer richness and composition on algal biomass in a closed and open marine system. *Ecology*, **88**, 178–187.

Mooney, H. & Hobbs, R.J. (2000) *Invasive Species in a Changing World*. Island Press, Washington, DC, USA.

Morris, W. (2003) Which mutualists are most essential? Buffering of plant reproduction against the extinction of pollinators. *The Importance of Species: Perspectives on Expendability and Triage* (eds P. Kareiva & S.A. Levin), pp. 260–280. Princeton University Press, Princeton, NJ.

Nwilene, F.E., Nwanze, K.F. & Youdeowei, A. (2008) Impact of integrated pest management on food and horticultural crops in Africa. *Entomologia Experimentalis et Applicata*, **128**, 355–363.

Oraze, M.J. & Grigarick, A.A. (1992) Biological control of ducksalad (*Heteranthera limosa*) by waterlily aphid (*Rhopalosiphum nymphaeae*) in rice (*Oryza sativa*). *Weed Science*, **40**, 333–336.

Paine, T.D. (2008) *Invasive Forest Insects, Introduced Forest Trees, and Altered Ecosystems: Ecological Pest Management in Global Forests of a Changing World*. Springer, Dordrecht, The Netherlands.

Pollet, A., Barragan, A.R. & Iturralde, P. (2004) *Conozca y Maneje la Polilla de la Papa. Seria de Divulgación*. Centro de Biodiversidad y ambiente – Escuela de Biologia PUCE, Ecuador.

Preisser, E.L., Lodge, A.G., Orwig, D.A. & Elkinton, J.S. (2008) Range expansion and population dynamics of co-occurring invasive herbivores. *Biological Invasions*, **10**, 201–213.

Roux, O. (1993) *Population ecology of potato tuber moth* Phthorimaea operculella *(Zeller) (Lepidoptera: Gelechiidae) and Design of an Integrated Pest Management Program in Tunisia*. Thesis. Swiss Federal Institute of Zurich, Zurich, Switzerland.

Savary, S., Elazeguia, F.A., Moodya, K., Litsingera, J.A. & Tenga, P.S. (1994) Characterization of rice cropping practices and multiple pest systems in the Philippines. *Agricultural Systems*, **46**, 385–408.

Sheldon, S.P. & Creed, R.P. (1995) Use of a native insect as a biological control for an introduced weed. *Ecological Applications*, **5**, 1122–1132.

Simberloff, D. (2006) Invasional meltdown 6 years later: important phenomenon, unfortunate metaphor, or both? *Ecology Letters*, **9**, 912–919.

Snyder, W.E., Snyder, G.B., Finke, D.L. & Straub, C.S. (2006) Predator biodiversity strengthens herbivore suppression. *Ecology Letters*, **9**, 789–796.

Thomas, M.B. (1999) Ecological approaches and the development of "truly integrated" pest management. *Proceedings of the National Academy of Sciences of the USA*, **96**, 5944–5951.

Vandermeer, J., Lawrence, D., Symstad, A. & Hobbie, S. (2002) Effects of biodiversity on ecosystem functioning in managed ecosystems. *Biodiversity and Ecosystem Functioning* (eds M. Loreau, S. Naeem & P. Inchausti), pp. 157–168. Oxford University Press, Oxford, UK.

Wilby, A. & Thomas, M.B. (2002) Natural enemy diversity and pest control: patterns of pest emergence with agricultural intensification. *Ecology Letters*, **5**, 353–360.

Willocquet, L., Aubertot, J.N., Lebard, S., Robert, C., Lannou, C. & Savary, S. (2008) Simulating multiple pest damage in varying winter wheat production situations. *Field Crops Research*, **107**, 12–28.

Zheng, Y., Daane, K.M., Hagen, K.S. & Mittler, T.E. (1993) Influence of larval food consumption on the fecundity of the lacewing *Chrysoperla carnea*. *Entomologia Experimental et Applicata*, **67**, 9–14.

Zwolfer, H. & Harris, P. (1971) Host speci- ficity determination of insects for biological control of weeds. *Annual Review of Entomology*, **16**, 159–178.

Received 23 March 2009; accepted 23 July 2009
Handling Editor: Andreas Erhardt

APPENDIX S11

Journal of Artificial Societies and Social Simulation **14** (3) 7
<http://jasss.soc.surrey.ac.uk/14/3/7.html>

Agent-based modeling of human-induced spread of invasive species in agricultural landscapes: insights from the potato moth in Ecuador

Rebaudo F.[1], Crespo-Pérez V.[1], Silvain J.F.[1], Dangles O.[1,2]

[1]IRD, UR 072, LEGS, UPR 9034, CNRS 91198 Gif-sur-Yvette Cedex and Université Paris-Sud 11, 91405 Orsay Cedex, France
[2]Pontificia Universidad Católica del Ecuador, Facultad de Ciencias Naturales y Biológicas, Quito, Ecuador.

Received: 27-Oct-2010   Accepted: 07-May-2011   Published: 30-Jun-2011

Abstract

Agent-based models (ABM) are ideal tools to deal with the complexity of pest invasion throughout agricultural socio-ecological systems, yet very few studies have applied them in such context. In this work we developed an ABM that simulates interactions between farmers and an invasive insect pest in an agricultural landscape of the tropical Andes. Our specific aims were to use the model 1) to assess the importance of farmers' mobility and pest control knowledge on pest expansion and 2) to use it as an educational tool to train farmer communities facing pest risks. Our model combined an ecological sub-model, simulating pest population dynamics driven by a cellular automaton including environmental factors of the landscape, with a social model in which we incorporated agents (farmers) potentially transporting and spreading the pest through displacements among villages. Results of model simulation revealed that both agents' movements and knowledge had a significant, non-linear, impact on invasion spread, confirming previous works on disease expansion by epidemiologists. However, heterogeneity in knowledge among agents had a low effect on invasion dynamics except at high levels of knowledge. Evaluations of the training sessions using ABM suggest that farmers would be able to better manage their crop after our implementation. Moreover, by providing farmers with evidence that pests propagated through their community not as the result of isolated decisions but rather as the result of repeated interactions between multiple individuals over time, our ABM allowed introducing them with social and psychological issues which are usually neglected in integrated pest management programs.

Keywords: agent-based modeling; socio-ecological systems; farmers; invasive pest; long distance dispersion; teaching.

Introduction

Agricultural systems are composed by two interlinked and interdependent subsystems, the social and the ecological subsystems, which co-evolve and interact at various levels and scales (Liu 2007). As a consequence, these systems are characterized by complex spatio-temporal dynamics and cultural variation (Papajorgji 2009). The management of agricultural invasive pests lies at the heart of such a complexity as pest propagation depends on both environmental features (e.g. climate, landscape structure) and farmers' behaviors (e.g. man-induced pest dispersion) (Epanchin-Niell 2010). The problems with dealing with multiple actors, non linearity, unpredictability, and time lags in invaded agricultural systems suggest that agent-based models (ABM) may have an important role to play in the sustainable development of farmers' practices to face those emergent threats (Berger 2001). Although ABM have increasingly been applied to physical, biological, medical, social, and economic problems (Bagni 2002; Bonabeau 2002; Grimm 2005) it has been, to our knowledge, disregarded by invasive pest management theory and practice.

Intrinsic dispersal capacities of agricultural invasive pest (in particular insects) are rarely sufficient to make them major threats at a large spatial scale. In most cases, invasive pest expansion is dependent on long-distance dispersal (LDD) events, a key process by which organisms can be transferred over large distances through passive transportation mechanisms (Leiboldt 2008). The study of the dynamics of pest dispersion in agricultural landscape is therefore comparable to that of disease contagion: as diseases, pests are transmitted from an infected person (farmer) to another who was previously "healthy", through different biological, social and environmental processes (Teweldemedhin 2004, Dangles 2010). Several studies have shown that the dynamics of infection spread involves positive and negative feedbacks, time delays, nonlinearities, stochastic events, and individual heterogeneity (Eubank 2004; Bauer 2009; Itakura 2010). Two factors have revealed particularly important to predict disease dynamics: 1) the number of encounter events between infected and healthy individuals, which mainly depends on individuals' mobility (Altizer 2006), and 2) the contamination rate between infected and healthy individuals, which depends on heterogeneous susceptibilities of individuals to be infected (Moreno 2002, Xuan 2009). Similarly, the spread of invasive pests throughout the agricultural landscape would depend on 1) movements of farmers carrying infested plants or seeds into new areas and 2) farmer's knowledge to detect the pest (pest control knowledge), therefore avoiding being infested and impeding the contamination of new areas (Dangles 2010).

Borrowing from disease contagion literature (e.g. Gog 2007; Yu 2010), we developed, using NetLogo (Wilensky 1999), an ABM to simulate the spread of an invasive potato insect pest in an agricultural landscape of the tropical Andes. Our model combined an ecological sub-model, simulating pest population dynamics driven by a cellular automaton including environmental factors of the landscape, with a social model in which we incorporated agents (farmers) potentially transporting and spreading the pest through displacements among villages. We then used our model for two purposes. First, we run the ABM under 10 levels of agents' (farmers) movements among villages and 7 levels of heterogeneity in farmer's pest control knowledge. We compared the resulting diffusion dynamics on the speed of pest spread, which represents a relevant metrics for invasive pest management by local stakeholders (e.g. the time available for agriculture officials to respond the threat). Second, we used our ABM as an education tool to increase farmer awareness on the importance of human-related LDD events of the pests which fostered the invasions of their valley (see Dangles 2010). While we specifically focused on an invasive insect pest in the tropical Andes in this paper, our approach to understand the influence of farmers' movements and pest control knowledge on pest dynamics and to transfer it through educational programs would be applicable to a much wider geographic and species range.

Study system

Our study deals with the potato tuber moth (*Tecia solanivora*), an invasive pest that has spread from Guatemala into Central America, northern South America and the Canary Islands during the past 30 years (Puillandre 2008). This pest attacks potato (*Solanum tuberosum*) tubers in the field and in storage and has become one of the most damaging crop pests in the North Andean region (Dangles 2008). Commercial exchanges of potato tubers at regional and local scales for both seeding and consumption are the main causes for the rapid expansion of the pest in all parts of the Ecuadorian highlands (2400-3500 m.a.s.l). These landscapes are characterized by highly variable environmental and social conditions due to steep altitudinal gradients and dispersed human settlement, respectively.

Model

Overall structure of the model

The socio-agronomical framework of the model consists in three key elements (Figure 1): 1) the agricultural landscape characteristics provided by a GIS environmental data base (Biodiversity Indicators for National Use, *Ministerio del Ambiente Ecuador and EcoCiencia* 2005), 2) the insect pest population, and 3) the groups of farmers. Pest dynamics in interaction with landscape features (e.g. land use, climate) is simulated through a cellular automaton (see the following sub-section). To transfer the cellular automaton into an agent-based simulation model we included farmers as agents acting individually upon pest dynamics in the agricultural landscape. Pests are therefore represented as a layer in the cellular automaton and farmers as agents in the ABM.

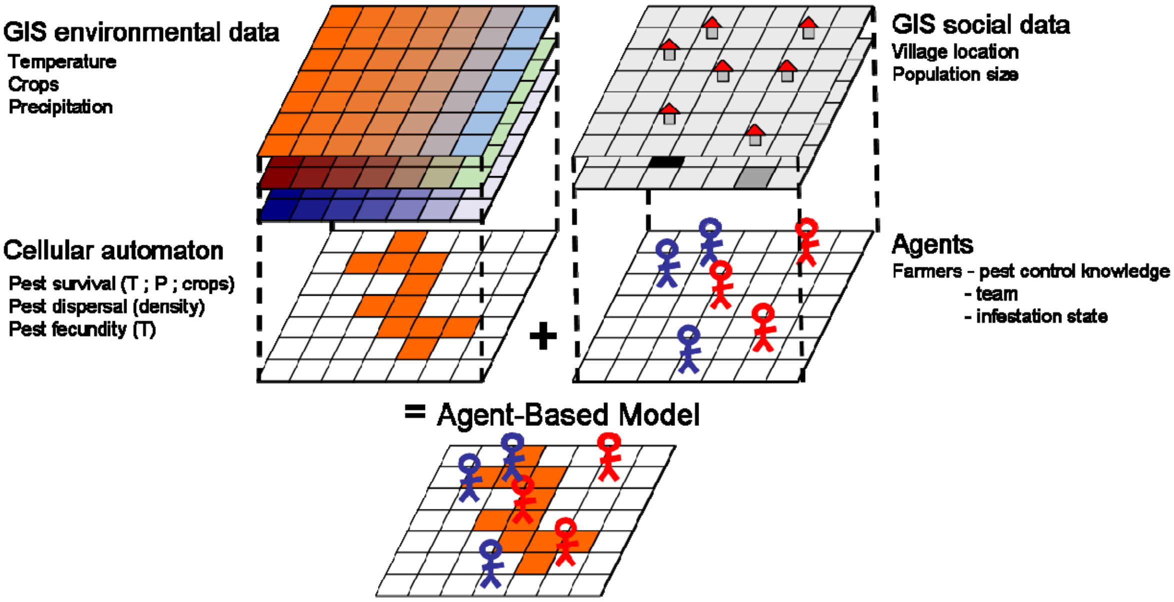


Figure 1. Schematic representation of the model structure

Modeling pest dynamics through cellular automata

The spatio-temporal dynamics of potato tuber moth is modeled through a simplified version of the cellular automaton developed by Crespo-Pérez (submitted). This model was developed with the CORMAS modeling platform (http://cormas.cirad.fr/en/applica/SimPolilla.htm) and is detailed in the Appendix 1. Briefly it is based on biological and ecological rules derived from field and laboratory experimental data for *T. solanivora*'s physiological responses to climate. Main processes include moth survival (climate dependent), dispersal through diffusion processes (density dependent), and reproduction (climate dependent). This model has been validated in a study area of 20 x 20 km within the remote valley of Simiatug in the Central Ecuadorian Andes (see section "teaching with the model") represented by a grid of 1,600 cells with a cell size of 0.25 km².

Modeling human-related pest dispersion through the agent-based model

The ABM aims at simulating the influence of farmers on the spatio-temporal dynamics of the potato moth. In this particular model, farmers are considered as potential agents for pest LDD, for example when they carry infested potato sacks from local markets to their home (other interactions with the pest, such as control by pesticide, are not included in this model). Their efficiency as LDD agents depends on their pest control knowledge: the higher their knowledge, the lower the probability they get their field infested after potato sacks transport (see below).

Agent process overview and scheduling

Agent process overview and scheduling are presented in figure 2. Agents move around on a grid of cells whose level of pest infestation is modeled by the cellular automaton (see Appendix 1). During each movement within a single timeframe agents turn "infested" (i.e. their potato crops are infested by the moth) or remain "non-infested" depending on their pest control knowledge and the pest infestation in a given cell. Each timeframe is equal to one moth generation (i.e. about 2 months) during which agents can move several times depending on their travel decisions. Agents with higher pest control knowledge (e.g. knowing how to recognize moth damage when they buy potato sacks at the market) have a lower probability of becoming infested. Then, agents move from one village to another to buy and/or sell potatoes. Agents' movements follow a gravity model (Rodrigue 2009), where the attractiveness of a village *i* compared to a village *j* is a function of both population size and cost-distance between them. Village infestation occurs when an infested agent move to a non-infested village (carrying infested potato sacks which will be used as potato seeds and thereby infest neighboring fields). Agent infestation occurs when a non-infested agent move to an infested village (buying infested potato seed sacks), depending on his pest control knowledge (higher pest control knowledge lead to lower probability of buying infested sacks).

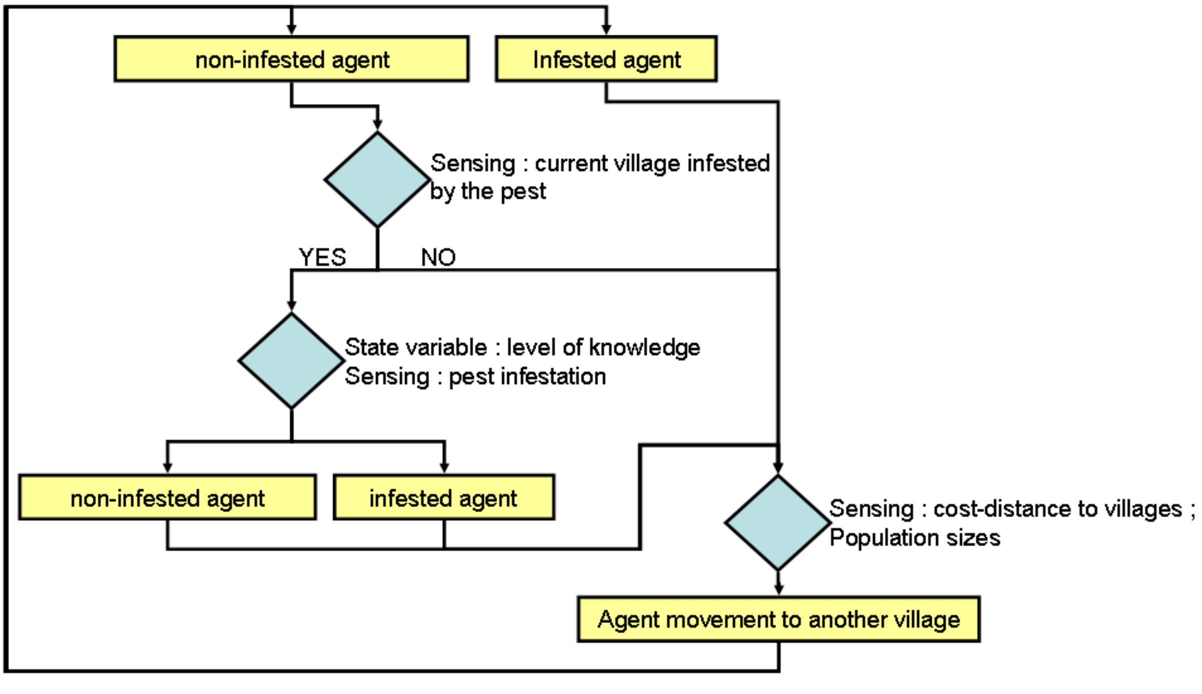


Figure 2. Agents' processes loop showing how farmers influence pest infestation spread. This loop is executed various times depending on farmers' traveling decisions during each timeframe.

Design concepts

Agents can sense the pest infestation of the cells but they do not use this information for their traveling decision. Instead, agents sense village population size and distance between villages so that they are able to perceive the relative cost/benefit of going to each village to sell/buy their crop: 1) it is less expensive to travel to closer villages and 2) more populated villages provide higher commercial opportunities. As a result, time needed to reach a complete pest infestation in the area emerges from a combination of purely biological pest dispersion, agents' movements from village to village and agent's pest control knowledge. A model example is available online at http://www.openabm.org (see "pest dispersion" by *innomip*).

Testing the effect of agents' movement and pest control knowledge on pest spread dynamics

Effect of agents' movements

We examined with our ABM how the number of agents' movements per generation would impact pest invasion dynamics. As we were interested in the early phases of invasions, which represent a relevant metrics for invasive pest management by local stakeholders, we used the time needed to reach 5% of infested cells as an outcome variable.

We found that increasing from 1 to 10 the number of agents' movements in the landscape had a negative exponential effect on the spread of the invasive pest (Figure 3 and animation in Appendix 2). Invasion speed was particularly increased up to 4 movements and then tended to stabilize. As expected, the effect of agents' movement on invasion speed was intensified by the number of agents located on the landscape, but once again this effect was not linear: insect pest dynamics was speeded up when adding up to 10 agents but remained roughly unchanged for the 10 following ones. For an intermediate scenario (4 movements, 10 agents), the speed of invasion was twice faster that of a purely biological spread (i.e. through insect's dispersion capabilities alone). The spatial configuration of the landscape is certainly linked to these results (see Figure 4 the frequency of visits of infested agents for each village), and the generation of random landscapes could help to quantify the landscape effect on agents' movements and so pest infestation, which hasn't been explored here.

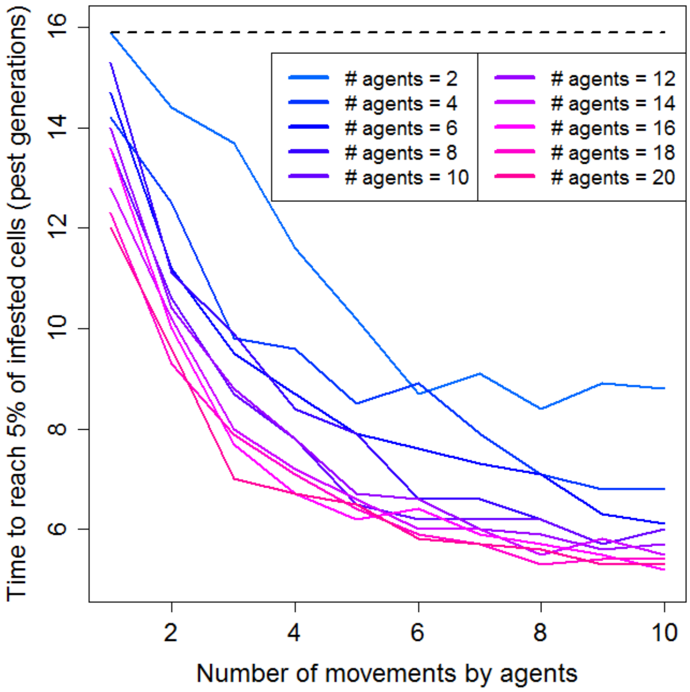


Figure 3. Influence of agents' movements (per pest generation) on pest infestation dynamics for different agent densities (n=2 to 20). The dashed line represents time needed to reach 5% of infested cells without agents (purely "biological" spread).

Our results highlight the importance of insect pest passive transportation by humans which allows invasive pests to make long-distance dispersal jumps. Even though several authors have acknowledged the significance of this type of dispersal for species spread, (e.g., Bossenbroek 2001, Suarez 2001) its inclusion in models still poses difficulties for modelers (Pitt 2009). Most dispersal models are based on empirically measured rates of pest dispersal, while in the case of LDD events it would be more useful to model human behaviors to better understand pest invasion dynamics. In this context, ABM offer an interesting yet poorly used method, to be applied to the vast field of biological invasions (see Luo 2010 and Vinatier 2009 for one of the rare study on exotic species using ABM, although in their case, agents are the invasive species). Results of our ABM simulations further revealed non linear processes between farmers' behavior (e.g. movement) and densities and pest spread, as already shown for disease expansion by epidemiologic models (e.g. Gog 2007). This suggests that a good understanding of social network structures would be a key step to better predict pest invasion speed in human dominated landscapes. In this context, ecologists would gain in following the path traced by epidemiologists with ABM to better understand the dynamics of invasive pests.

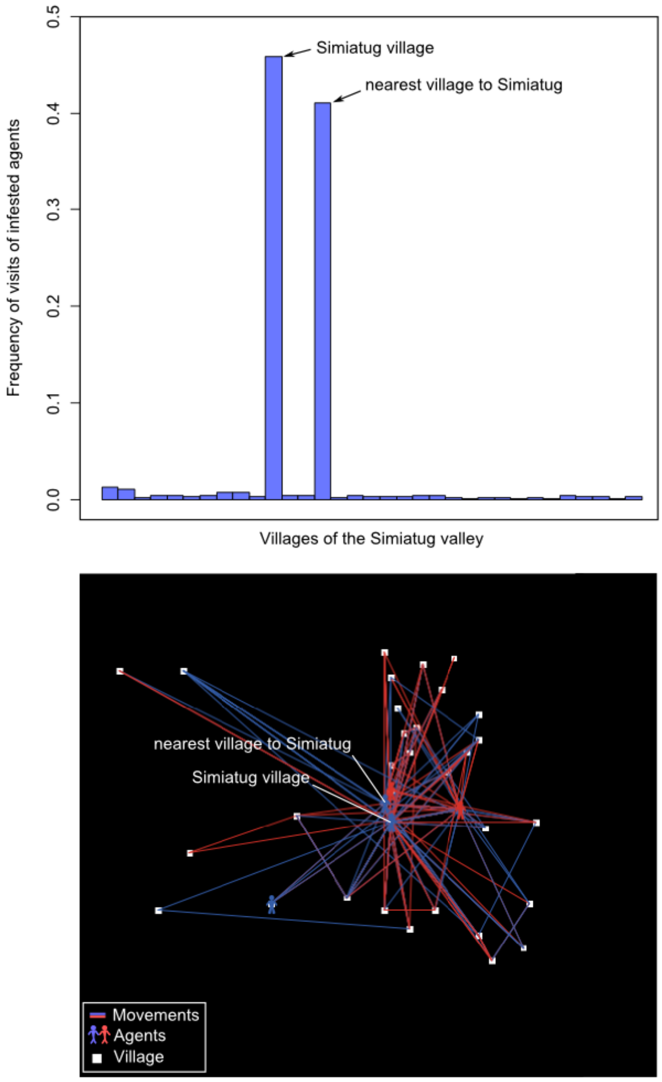


Figure 4. Frequency of visits of infected agents for each village and map of the Simiatug valley with agents' movements and villages localization.

Effect of agent's heterogeneity in pest control knowledge

We then explored with our ABM how agents' pest control knowledge (ranked from 0 to 100) would impact pest propagation dynamics. As pest control knowledge was usually variable among farmers (Dangles 2010), we were interested in examining the influence of heterogeneous levels among agents on pest spread dynamics. To achieve this goal, we tested 7 levels of heterogeneity (standard deviation = 0, 5, 10, 15, 20, 25, 30) around 10 mean values of pest control knowledge (mean = 0 to 100). For each simulation, agents' pest control knowledge levels were randomly chosen from a Normal distribution, N(mean, standard deviation).

Our simulations revealed that agents' pest control knowledge had a significant effect on pest invasion dynamics (Figure 5 and animation in Appendix 3). In all simulations, lower agents' pest control knowledge led to higher invasion speed, almost twice faster than intrinsic pest dispersion spread for highest infectivity values. Agents' movement had a worsening effect, with faster invasion occurring for higher agent's mobility. Agents' heterogeneity in pest control knowledge had a weak effect on pest dynamics, especially for high agents' mobility (6 and 4). However, heterogeneity in knowledge did introduce some sochasticity in invasion dynamics when agents seldom moved.

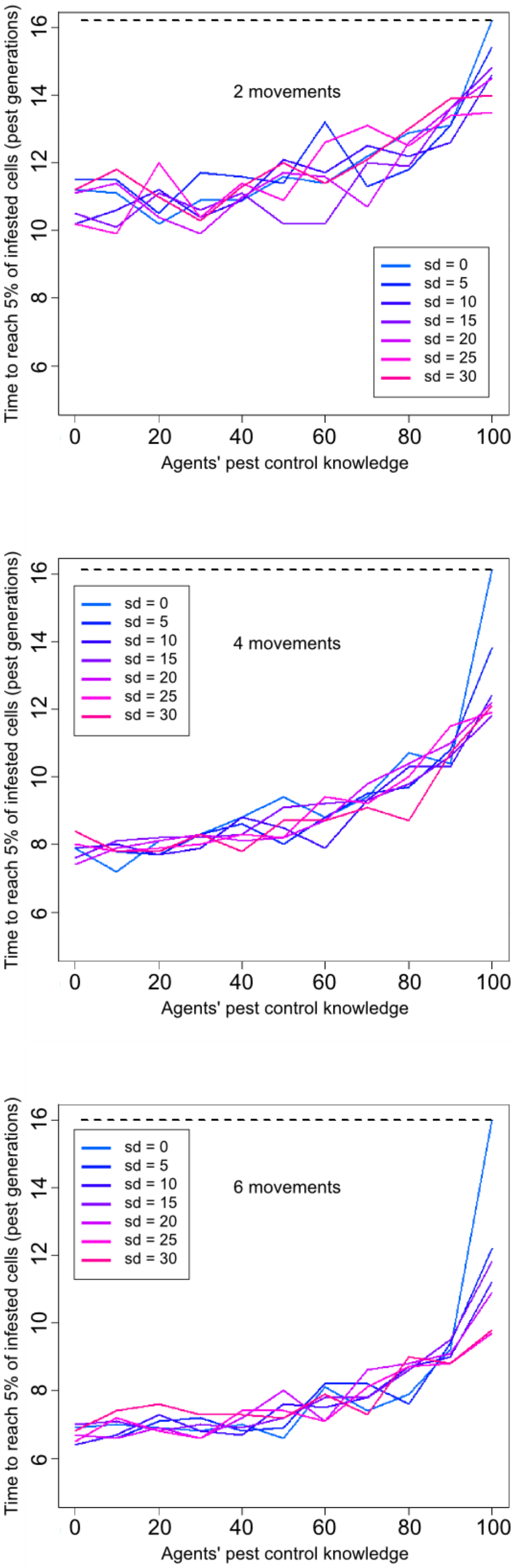


Figure 5. Influence of agents' pest control knowledge (means) and heterogeneity (standard deviation = 0 to 30%) on pest infestation dynamics for three frequencies of movements (6, 4, and 2). The dashed line represents time needed to reach 5% of infested cells without agents (purely "biological" spread).

As reported by epidemiologists for disease spread (e.g., Newman 2002), our results showed that agents' pest control knowledge had an important impact on the dynamics of pest invasion spread. This suggests that farmers' pest control knowledge would be a key, yet poorly studied, variable to take into account for modeling pest invasions in agricultural landscapes. Less expectedly, we found that heterogeneity of knowledge among agents had a relatively weak effect on pest dynamics, especially for high mobility levels of agents. This contrast with epidemiological models which have generally shown that heterogeneous populations enhance the spread of infections as well as make them harder to eradicate (for a review see Anderson 1992). One potential explanation is that the limited number of villages used in our study favor infestation mixture among agents and rapidly smooth up its impact on invasion spread dynamics. However, our results showed that when all agents are "healthy" (pest control knowledge = 100), any addition of agents with lower levels of knowledge will considerably speed up pest dynamics (especially at high levels of movements), thereby confirming predictions of disease spread theory.

Teaching with the model

In a second step, we used our ABM as an educational tool to teach farmers about potential invasion risks resulting from individual behaviors. Teaching activities were realized in February 2009 at the Agriculture and Technology College of the Simiatug valley in the central Ecuadorian Andes. This parish is comprised of roughly 45 kichwa communities living between 2800 m and 4250 m of altitude, that share similar characteristics in terms of social organization, date of establishment, and agricultural practices. Currently, about 25,000 people, mainly subsistence and market-oriented farmers, live in the Simiatug parish. The main agricultural products are pasture, cereals (barley), legumes (fava bean) and potatoes as well as cattle and sheep (see more details in Dangles 2010). Although the remoteness of the valley protects it against moth invasion, increasing commercial exchanges from and to Simiatug are currently increasing the risk of moth introduction. Local farmers were therefore interested in learning about potential risks associated with the pest and how to control their spread in the valley.

Model introduction to the farmers

Introduction of the models and variable representation to the farmers has been a long process that began with the educational program set up in 2007 (Dangles 2010, see the timeline of the ground work in Figure 6).

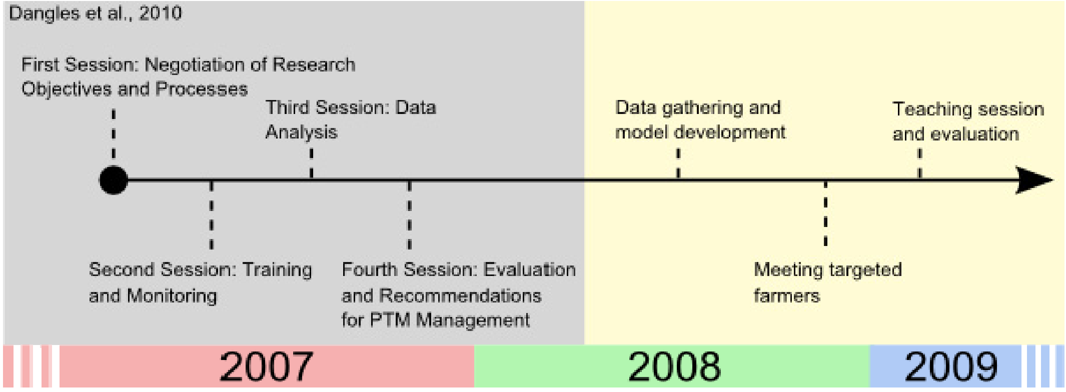


Figure 6. Timeline of the groundwork prior to the teaching session

For this program, we held a negotiation session to insure that teaching was driven by farmers' interests followed by a training session on integrated pest management and on participatory monitoring of potato moth in the valley. After the data analysis session, farmers had acquired a rather clear connection between pest abundance and air temperature, village size and remoteness (see Dangles 2010, for a detailed description of the sessions with farmers). This initial process allowed us to introduce our model in a second step and to use it as a teaching tool. Farmers were young (17 to 25 years old) and showed innate interest in "playing" with the computers and seeing simulations (an Internet café just opened in Simiatug the year before starting the ABM teaching session). The model was presented as a way to better understand a result that farmers themselves had found: the importance of LDD in moth dispersion (see Dangles 2010).

Model parameterization

For teaching purposes, farmers were separated into two, "blue" and "red" teams; having two teams that compete for minimization of pest presence in the valley stimulated enthusiasm among farmers. Each member of the team was asked to fill a questionnaire including 20 items, 10 on basic issues (biology and ecology of the pest) and 10 on applied issues (pest management). A facilitator helped the players to fill in these questionnaires. Based on filled questionnaires, we built a "pest control knowledge index" for each farmer, which corresponded to the percent of questions answered correctly. Farmers were also asked to answer questions about their travel behavior in the valley (destination and frequencies). Villages' locations and population sizes were defined by farmers using maps (see figure 7). Environmental data such as temperature or precipitation were updated using real values in the considered area (Dangles and Carpio, unpublished data provided with the model in the openabm.org website).

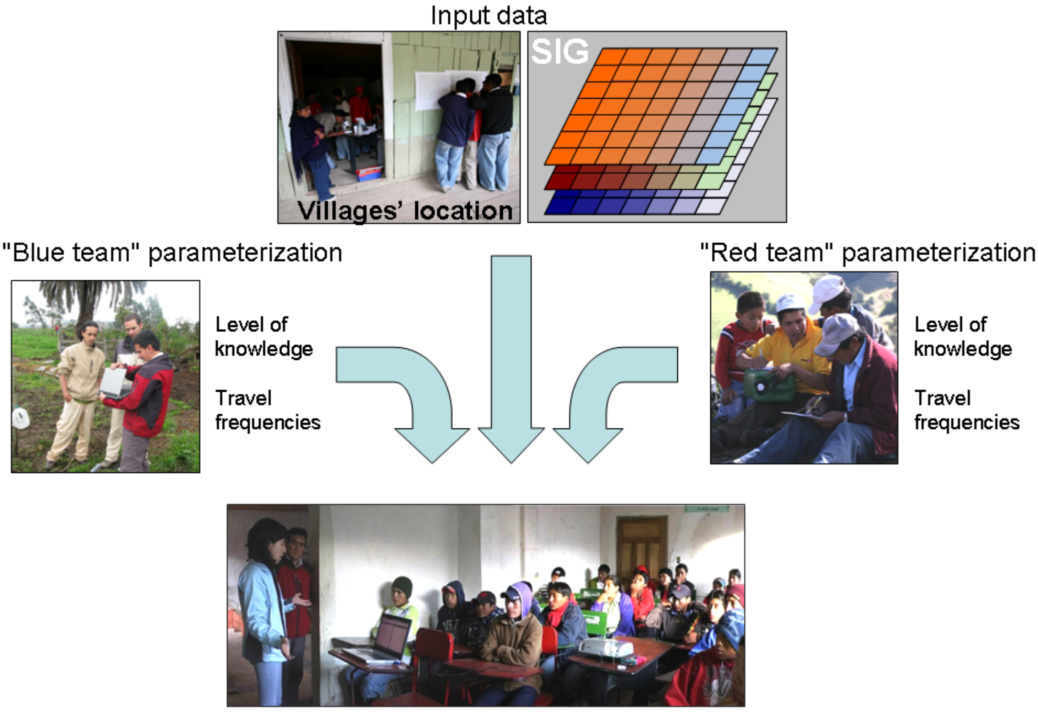


Figure 7. Teaching with an agent-based model in an agricultural valley of Ecuador

Playing and learning with the agent-based model

Once input data were collected and set up (Table 1), we ran the model and registered the spread of the pest throughout the valley. In all simulations, agents are randomly located at the beginning of the run.

Table 1. Parameters and simulation results of the gaming session with farmers.

Parameters	Parameters values used for the gaming session	Parameters values at the end of the gaming session
Parameterization		
Number of farmers (agents)	10	10
Number of agents' movements per timeframe (pest generations)	6	3
Pest control knowledge (following a Normal distribution ~N(mean, sd))	~N(0.4;0.1)	~N(0.8;0.1)
Results		
Time needed for complete infestation (pest generation)	39	45

Our model output could separate between 1) cells infested due to LDD events made by the blue team, 2) cells infested by red team LDD and 3) cells infested by insect's own dispersal capabilities (see http://www.openabm.org; see "pest dispersion" by *innomip*). Each team was therefore able to visualize its relative impact on moth dispersion throughout the Simiatug valley through the main color of a spatial interface representing the landscape. They were further invited to "play" with the simulation interface by changing LDD and the pest control knowledge values and to see the consequences in terms of moth spread throughout their valley. A synthesis of the processes involved in the teaching session (including required time) is given in Table 2.

Table 2. Processes and time required for teaching and learning

Gaming session process	Main activities	Time spent
Introduction	Overall presentation of all actors	1 hour
Computer presentation	Presentation of computer simulation utility	30 minutes
Model adoption: building community map (villages and populations)	Presentation of the spatial representation of the model	30 minutes
Model input variables (interviews)	Model parameterization	1 hour
Model output variables	Running the model with the two teams, result presentation and discussion	1 hour
Playing session 1: farmer movements and pest infestation spread	Farmer teams modify agents' movements and visualize consequences on pest spreading	30 minutes
Playing session 2: farmer knowledge and pest infestation spread	Farmer teams modify agents' pest control knowledge and visualize consequences on pest spreading	30 minutes
Conclusion and evaluation	General discussion with farmers and interviews	1 hour

Model adoption

Because participants were young farmers we had no problem related to potential technical, cultural, knowledge or attitude barriers. One of the main difficulties related to model adoption turned out to be the spatial representation of farmer's villages, which was partially solved by building with them a digital map of their valley. Another difficulty was that farmers had a hard time in associating grid cell colors with the presence of moths. Unfortunately, we could not fix this problem during the teaching session and this was probably one of the main drawbacks of our approach. However, since this date, we improved the simulation to integrate the drawing of moths spreading on the cellular automata grid in a simple model aimed at improving its adoption (see http://www.openabm.org see "pest dispersion version 1" by *innomip*).

Benefits of model-based teaching to farmers

At the end of the session we re-evaluated participant pest control knowledge on basic and practical moth control issues with the same 20-item indicators questionnaire (see above). The mean pest control knowledge (percent of questions answered correctly) increased from 40 ± 10 (basic) and 40 ± 20 (practical) at the beginning of the session to 80 ± 10 (basic), and 80 ± 10 (practical) at the end of the session, suggesting that farmers would be able to better manage pest risks after the teaching sessions. As a whole, our educational program (2007-2009) indeed enhanced local awareness about the need to control the pests before they became too numerous and covered the whole landscape. The main specific management decision taken by farmers was a promise to systematically check for moth infestation when buying potato tubers in the Simiatug market before transportation to their community (see also Dangles 2010). Although farmers vouched for model's attractiveness and usefulness to learn about pest problems, it remained hard to quantify knowledge enhancement specifically due to the ABM as opposed to that due to the rest of the educational participatory program. However, we believe that the use of ABM and computers significantly complemented our educational program on pest management in the valley as it had a clear consequence in enhancing young farmers' interest in agricultural issues. The College of Simiatug indeed suffered from an increasing lack of interest from students of agriculture disciplines in favor of technical/computational ones. Our program showed young farmers that both disciplines could be merged and that they could find through the Internet (http://www.innomip.com) computational tools to increase their knowledge on pest management. Our study is a preliminary approach in the use of ABM for pest management issues. Further efforts should be done to optimize model adoption process such as the early identification of gaps in farmers' knowledge (Wilson 2009), the consideration of peak-labor periods (White 2005) or the social network of learners (Boahene 1999).

Another achievement of ABM was that, by providing farmers with evidence that pests propagated through their community not as the result of isolated decisions by individuals but rather as the result of repeated interactions between multiple individuals over time, our ABM pointed at key psychological and social issues, highly relevant for efficient management of invasive pests (Peshin 2008). ABM may therefore be a powerful tool to advance the application of social psychology theory by stakeholders in rural communities (Smith 2007) and to change individual attitudes (Jacobson 2006). This suggests that new approaches in pest management extension practices should include topics such as group decision making, intergroup relation, commitment, and persuasion which deal directly with how other farmers influence one's thoughts and actions (Mason 2007; Urbig 2008). By examining group- and population-level consequences on invasion process, agent-based modeling may therefore reveals as a powerful pedagogical approach to change behaviors across large populations, a long lasting issue in pest management outreach programs worldwide (Feder 2004).

Conclusion

We showed in this study that agent-based modeling may be a powerful tool to simulate invasive pest spread in human dominated landscapes. Our simulations further revealed that both farmers' movements and pest control knowledge could significantly impact invasion speed and should be considered as key variables to better predict pest invasion dynamics in agricultural landscapes. Regarding the use of ABM as educational tools, we found that new technologies (computers) increased the interest of young farmers in learning about how to better face pest problems. Although we would need to design proper studies to better understand the specific ways ABM fosters learning processes, the introduction of ABM into learning environments located in remote places may promise to improve education of farmers, especially young ones. For example, ABM can be integrated into interactive websites or burned on a CD and be available to farmer communities in which technology access increases rapidly thanks to governmental initiatives. In view of the growing threat made by emergent insect pests worldwide, especially in remote and poor localities, further efforts to include cost-efficient ABM into integrated pest management programs may represent a promising line of research and applications.

Appendices description

Appendix 1. Description of the cellular automaton used to simulate the pest model using the ODD protocol (Grimm 2006).

From Appendix 2 to 4, representing animated simulations, blue and red figurines represents agents, and blue and red links agents' movements form village to village. The number in the top right corner corresponds to the number of timeframe and the background color to the pest infestation (black: no pest infestation ; green: pest infestation due to purely biological diffusion ; red and blue: pest infestation due to an infected agent movement). At the end of each animated simulation, the area to the right remains uninfected. This area corresponds to higher elevations where the pest can not survive.

Appendix 2. Animated simulations showing the effect of agents' movements on the pest spread with 2 movements per timeframe and 6 movements per timeframe. The pest infestation is quicker when agents move more.

Appendix 3. Animated simulations showing the effect of agents' pest control knowledge without heterogeneity on the pest spread with a mean pest control knowledge of 0 and 100. When the pest control knowledge is high, the pest can only disperse through diffusion (i.e. very slowly), compared to a simulation when pest control knowledge is low, where the agents' behaviors lead to a full infestation by long distance dispersal events form village to village.

Appendix 4. Animated simulation of the game session. Parameters are presented in Table 1. The simulation ran to reach full infestation of the landscape suitable for the pest. Integrating real distribution of pest control knowledge (Normal distribution), we observed that almost all the landscape is infested due to long distance dispersal events. It revealed the importance to focus on pest control knowledge reinforcement to reduce the incidence of the pest at the landscape level.

Acknowledgements

We thank two anonymous reviewers for their helpful comments on a previous version of this work. We are grateful to Claire Nicklin, from the McKnight Foundation, for the linguistic revision of the manuscript. We also thank Carlos Carpio and Mario Hererra for their technical support and all farmers involved in this process. This study was part of the research conducted within the project *Innovative Approaches for integrated Pest Management in changing Andes* (C09-031) funded by the McKnight Foundation. VCP received the financial support of the *Direction Soutien et Formation* of the IRD through a Ph.D. grant (2009-2011).

References

ALTIZER, S, Dobson, A, Hosseini, P *et al* (2006). Seasonality and the dynamics of infectious diseases. *Ecology Letters* : 9:467-84.

ANDERSON, RM and May, RM (1992). Infectious diseases in humans (*Oxford University Press*, Oxford, 1992).

BAGNI, R, Berchi, R and Cariello, P (2002). A comparison of simulation models applied to epidemics. *Journal of Artificial Societies and Social Simulation* vol. 5 (, no. 3) 5 http://jasss.soc.surrey.ac.uk/5/3/5.html.

BAUER, AL, Beauchemin, CAA and Perelson, AS (2009). Agent-based modeling of host-pathogen systems: The successes and challenges. *Information Sciences* 179: 1379–1389.

BERGER, T (2001). Agent-based spatial models applied to agriculture: a simulation tool for technology diffusion, resource use changes and policy analysis. *Agricultural Economics* 25 245–260.

BOAHENE, K and Snijders, TAB (1999). An Integrated Socioeconomic Analysis of Innovation Adoption: The Case of Hybrid Cocoa in Ghana. *Journal of Policy Modeling* 21, 167-184.

BONABEAU, E, (2002). Agent-based modeling: methods and techniques for simulating human systems, *PNAS* 99, 7280-7287.

BOSSENBROEK, JM, Kraft, CE and Nekola, JC (2001). Prediction of long-distance dispersal using gravity models: Zebra mussel invasion of inland lakes. *Ecological Applications* 11, 1778-1788.

BRUSH, SB (2004). Farmer's bounty. *Yale University Press.*

CRESPO-PEREZ, V, Rebaudo, F, Silvain, JF, and Dangles, O (submitted). Invasive insect spread in a mountainous, socio-ecological landscape of Ecuador. Submitted to *Landscape Ecology*.

DANGLES, O, Carpio, C, Barragan, AR, Zeddam, JL and Silvain, JF (2008). Temperature as a key driver of ecological sorting among invasive pest species in the tropical Andes. *Ecological Applications* 18, 1795–1809.

DANGLES, O, Carpio, FC, Villares, M, Yumisaca, F, Liger, B, Rebaudo, F and Silvain, JF (2010). Community-based participatory research helps farmers and scientists to manage invasive pests in the Ecuadorian Andes. *Ambi*o: A Journal of the Human Environment, 39, 325-335.

DANGLES, O, Mesías, V, Crespo-Perez, V and Silvain, JF (2009). Crop damage increases with pest species diversity: evidence from potato tuber moths in the tropical Andes. *Journal of Applied Ecology* 46, 1115-1121.

DARE, W and Barreteau, O (2003). A role-playing game in irrigated system negotiation: between play and reality. *Journal of Artificial Societies and Social Simulation* 6, <http://jasss.soc.surrey.ac.uk/6/3/6.html>

EPANCHIN-NIELL, RS, Hufford, MB, Aslan, CE, Sexton, JP, Port, JD and Waring, TM (2010). Controlling invasive species in complex social landscapes. *Front Ecol Environ* 8: 210–216.

EUBANK, S, Guclu, H, Kumar, VSA, Marathe, MV, Srinivasan, A, Toroczkai, Z and Wang, N (2004). Modelling disease outbreaks in realistic urban social networks. *Nature* 429 180-184.

FEDER, G, Just, RE and Zilberman, D (1985). Adoption of Agricultural Innovations in Developing Countries: A Survey. *Economic Development and Cultural Change* 33, 255-298.

FEDER, G, Murgai, R, and Quizon, J (2004). The acquisition and diffusion of knowledge: The case of pest management training in farmer field schools, Indonesia. *Journal of Agricultural Economics* 55, 217–239.

GILBERT, M, Gregoire, JC, Freise, JF and Heitland, W (2004). Long-distance dispersal and human population density allow the prediction of invasive patterns in the horse chestnut leafminer Cameraria ohridella. *Journal of Animal Ecology* 73 3, 459-468.

GONG, X and Renbin, X (2007). Research on Multi-Agent Simulation of Epidemic News Spread Characteristics. *Journal of Artificial Societies and Social Simulation* 10 (3) 1 vol. 10, no. 31. http://jasss.soc.surrey.ac.uk/10/3/1.html.

GRIMM, V *et al.* (2005). Pattern-oriented modeling of agent-based complex systems: lessons from ecology. *Science* 310: 987–991.

GRIMM V, Berger U, Bastiansen F, Eliassen S, Ginot V, Giske J, Goss-Custard J, Grand T, Heinz S K, Huse G, Huth A, Jepsen J U, Jørgensen C, Mooij W M, Müller B, Pe'er G, Piou C, Railsback S F, Robbins A M, Robbins M M, Rossmanith E, Rüger N, Strand E, Souissi S, Stillman R A, Vabø R, Visser U and DeAngelis D L (2006). A standard protocol for describing individual-based and agent-based models. *Ecological Modelling* 198 (1-2), 115-126.

ITAKURA, J, Kurosaki, M, Itakuraa, Y, Maekawab, S, Asahinaa, Y, Izumi, N and Enomoto N (2010). Reproducibility and usability of chronic virus infection model using agent-based simulation; comparing with a mathematical model. *Biosystems* 99: 70-78.

JACOBSON, SK, McDuff, MDD and Monroe, MC (2006). Conservation education and outreach techniques. *New York: Oxford University Press, Inc*.

LIEBHOLD, AM and Tobin, PC (2008). Population ecology of insect invasions and their management. *Annual Review of Entomology*, 53: 387-408.

LIU, J *et al.* (2007). Complexity of Coupled Human and Natural Systems. *Science* 317: 1513-1516.

LUO, M, Opaluch JJ (2010). Analyze the risks of biological invasion: An agent based simulation model for introducing non-native oysters in Chesapeake Bay, USA. *Stoch Environ Res Risk Assess*, DOI 10.1007/s00477-010-0375-2

MASON, WA, Conrey, FR, and Smith, ER (2007). Situating social influence processes: Dynamic, multidirectional flows of influence within social networks. *Personality and Social Psychology Review*, 11(3), 279–300.

MORENO, Y, Pastor-Satorras, R and Vespignani A (2002). Epidemic outbreaks in complex heterogeneous networks, *Eur. Phys. J. B* 26 (2002) 521–529.

NEWMAN, MEJ (2002). Spread of epidemic disease on networks, *Phys. Rev.* E 66, 016128-1 :11.

PAPAJORGJI, PJ and Pardalos PM (2009). Advances in Modeling Agricultural Systems, *Springer Publishing Company*, NY.

PESHIN, R and Dhawan, AK (2008). Integrated pest management: dissemination and& impact, *Springer* 550p.

PITT, JPW, Worner, SP and Suarez, AV (2009). Predicting Argentine ant spread over the heterogeneous landscape using a spatially explicit stochastic model. *Ecological Applications* 19, 1176-1186.

PUILLANDRE, N, Dupas, S, Dangles, O, Zeddam, JL, Capdevielle-Dulac, C, Barbin, K, Torres-Leguizamon, M and Silvain, JF (2008). Genetic bottleneck in invasive species: the potato tuber moth adds to the list. *Biological Invasions* 10, 319-333.

RODRIGUE, JP, Comtois, C and Slack, B (2009). The Geography of Transport Systems. *Routledge*, May 2009, pp. 368.

SMITH, ER and Conrey, FR (2007). Agent-based modeling: A new approach for theory-building in social psychology. *Personality and Social Psychology Review*, 11, 87-104.

SUAREZ, AV, Holway, DA and Case, TJ (2001). Patterns of spread in biological invasions dominated by long-distance jump dispersal: Insights from Argentine ants. *Proc Natl Acad Sci U S A*, 98, 1095-1100.

TEWELDEMEDHIN, E, Marwala, T and Mueller, C (2004). Agent-based modelling: a case study in HIV epidemic. *Proceedings of the 4th International Conference on Hybrid Intelligent Systems (HIS'04)*; Washington, DC, USA. IEEE Computer Society; 2004. pp. 154–159.

URBIG, D, Lorenz, J and Herzberg, H (2008). Opinion Dynamics: the Effect of the Number of Peers Met at Once. *Journal of Artificial Societies and Social Simulation* 11 (2) 4vol. 11, no. 2 4, http://jasss.soc.surrey.ac.uk/11/2/4.html.

VINATIER, F, Tixier, P, Le Page, C, Duyck, PF and Lescourret, F (2009). COSMOS, a spatially explicit model to simulate the epidemiology of *Cosmopolites sordidus* in banana fields. *Ecological Modelling* 220, 2244-2254.

WHITE, DS, Labarta, RA and Leguia, EJ (2005). Technology adoption by resource-poor farmers: considering the implications of peak-season labour costs. *Agricultural Systems* 85, 183-201.

WILENSKY, U (1999). NetLogo. http://ccl.northwestern.edu/netlogo. Center for Connected Learning and Computer-Based Modeling. Northwestern University, Evanston, IL.

WILSON, RS and Hooker, N (2009). Targeting the farmer decision making process: A pathway to increased adoption of integrated weed management. *Crop Protection* 28, 756-764.

XUAN, H, Xu, L and Li, L (2009). A CA-based epidemic model for HIV/AIDS transmission with heterogeneity. *Annals of Operation Research* 168: 81–99.

YU, B, Wang, J, McGowan, M, Vaidyanathan, G and Younger, K (2010). Gryphon: A Hybrid Agent-Based Modeling and Simulation Platform for Infectious Diseases. *Advances in Social Computing* 6007/2010, 199-207.

Modelando la propagación de plagas invasoras

Por Verónica Crespo-Pérez, François Rebaudo, Olivier Dangles
(verocrespoperez@yahoo.com), (rebaudo@gmail.com), (Olivier.Dangles@legs.cnrs-gif.fr)

Siempre han existido las invasiones biológicas

Las invasiones biológicas no son una novedad. Los registros fósiles indican que los rangos de distribución de las especies han estado siempre en un flujo constante. Incluso, hace cientos de millones de años con el choque o separación de los continentes, los cambios de clima y el retroceso de los océanos, los rangos de distribución cambiaban resultando en muchos casos en introducciones de especies a comunidades donde antes no estaban. Sin embargo, cuando hablamos de invasión, la mayoría de los biólogos piensa en las invasiones biológicas contemporáneas mediadas en su mayoría por las actividades humanas que aceleran y facilitan la introducción de especies en lugares más alejados de aquellos a los que podrían dispersarse naturalmente. Aunque el hombre ha estado moviendo plantas y animales entre ecosistemas por miles de años, las tasas de invasión han aumentado dramáticamente con la evolución de los avances tecnológicos. Estos adelantos, especialmente aquellos relacionados con las actividades agrícolas, de recreación y de transporte, han permitido a las especies sortear barreras antes infranqueables a velocidades antes inimaginables.

Etapas en la dinámica de las invasiones biológicas

Existen tres etapas: 1) la introducción de una o varias poblaciones foráneas a un área nueva, 2) el establecimiento de poblaciones viables, su proliferación, y 3) su integración en el área de introducción con sus eventuales impactos. A pesar de que la mayor parte de las especies introducidas desaparecen sin poder establecerse o proliferar en el nuevo ambiente, aquellas que lo logran pueden producir graves impactos sobre la salud y la economía humana y sobre la biodiversidad y el funcionamiento de los ecosistemas nativos. Gran parte de las plagas agrícolas y forestales más devastadoras son especies invasivas. Los insectos son uno de los grupos con la más alta capacidad colonizadora y poseen diversas estrategias que facilitan su establecimiento como una reproducción tipo r (producción de un gran número de descendientes a los que se dedica pocos esfuerzos), pupación, diapausa, creación de un microclima y régimen trófico generalista. Además, al estar libres de predadores o competidores en el nuevo ambiente, estas especies pueden propagarse con gran facilidad. Dada la gran cantidad de perjuicios económicos causados por los insectos invasores, no sorprende la gran cantidad de estudios sobre las características de dispersión y la ecología de las poblaciones invasoras. Pero tampoco sorprende que la mayoría de estudios se centren sobre especies invasoras de las zonas templadas y muy pocos de zonas tropicales. La falta de estudios y el reducido manejo de las especies invasoras en estas zonas producen grandes pérdidas económicas, principalmente en las regiones más pobres. Es muy importante un entendimiento más profundo de los mecanismos y la dinámica de las invasiones para poder así manejarlas y reducir su impacto.

El modelamiento de la propagación de las plagas invasoras permite comprender, simular, predecir y controlar su expansión. Inicialmente se utilizaban modelos muy simples de movimiento al azar ("random walk models") o de difusión que consideraban que las poblaciones se expandían por simples movimientos aleatorios de sus integrantes. Sin embargo, los organismos no eligen al azar la dirección hacia la que se van a mover. Al contrario, éstos pueden cambiar la velocidad o dirección a la que se mueven debido a diferencias topográficas, climáticas o de su fisiología, edad, tamaño, comportamiento o experiencia previa. Por esto, los modelos más recientes intentan tomar en cuenta la mayor cantidad posible de estos factores para una simulación más robusta y realista, pero la complejidad de los procesos biológicos implicados en la propagación de plagas invasoras hace que ésta sea muchas veces numéricamente inextricable.

Los autómatas celulares

Un método potencial para simplificar y entender los procesos de expansión de las especies invasivas es el uso de modelos Autómatas Celulares (A.C.). Un autómata celular es un modelo matemático para un sistema dinámico que evoluciona en pasos discretos. Gracias a su relativamente fácil implementación, su habilidad de replicar formas espaciales y de ser incorporado en sistemas de información geográfica (SIG) los modelos A.C. han sido aplicados ampliamente en diversos problemas ecológicos como la propagación de epidemias, la dinámica de bosques, el crecimiento urbano y los cambios en el uso de tierras. Sin embargo, su aplicación directa con problemas de especies invasoras es aún rara.

Un Autómata Celular tiene las siguientes características:

1. El espacio está formado por un conjunto finito de celdas distribuidas en una rejilla regular n-dimensional. Si el autómata es unidimensional las celdas se distribuyen a lo largo de una línea, si es bidimensional a través de una rejilla plana que puede ser triangular, rectangular, cuadrada, hexagonal, etc.

2. Cada celda puede estar en un único estado en determinado instante de tiempo.

3. El estado de las celdas cambia de un instante a otro de acuerdo a un conjunto de reglas de evolución comunes a todas las celdas.

4. Estas reglas son esencialmente una máquina de estado finito, usualmente especificadas en una tabla de reglas (también conocida como función de transición), con una entrada para todas las posibles configuraciones del vecindario.

5. El vecindario de una celda está formado por las celdas adyacentes y se define igual para todas las celdas del autómata.

El Juego de la Vida ("The Game of Life"), diseñado por el matemático británico John Horton Conway en 1970, es el mejor ejemplo de un autómata celular. A pesar de que la mayoría de autómatas celulares desarrollados últimamente son mucho más complejos que el Juego de la Vida una breve explicación de cómo éste opera nos puede ayudar a entender la manera de operar de estos modelos. El modelo ocupa una cuadrícula bidimensional donde se coloca al inicio un patrón cualesquiera de celdas con el estado "célula viva" o "célula muerta." En efecto una celda puede tener sólo un estado. La vecindad para cada célula son los ocho vecinos a su alrededor. De manera repetida, se aplican simultáneamente sobre todas las células de la cuadrícula las siguientes 3 reglas:

1. Nacimiento: se reemplaza una célula muerta por una viva, si dicha célula tiene exactamente 3 vecinos vivos.
2. Muerte: se reemplaza una célula viva por una muerta, si dicha célula no tiene más de 1 vecino vivo (muerte por aislamiento) o si tiene más de 3 vecinos vivos (muerte por sobrepoblación).
3. Supervivencia: una célula viva permanecerá en ese estado, si tiene 2 ó 3 vecinos vivos.

En la figura 1 se presenta un ejemplo de la transición de diversas celdas durante 4 generaciones. En primer lugar observamos que las celdas 3, 15, 23 y 11, muertas en la primera generación, se vuelven vivas en la siguiente por tener exactamente 3 vecinas vivas. Las celdas 8, 12, 13, 14 y 18 en cambio, mueren debido a superpoblación a su alrededor (más de tres vecinas vivas). Por último las celdas 7, 9, 17 y 19 permanecen vivas. La figura

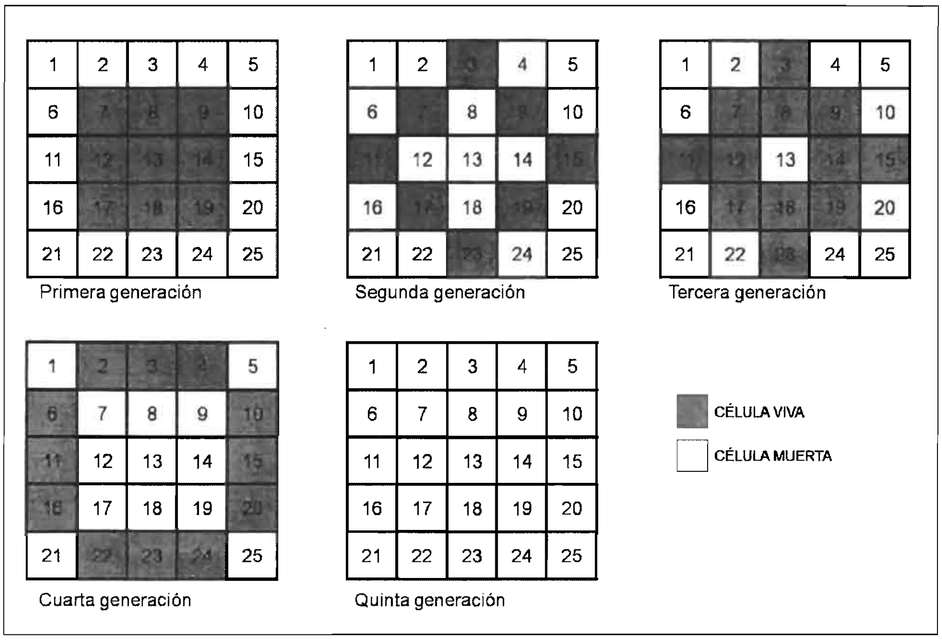


Figura 1. Esquema que muestra la dinámica de las celdas con el estado "célula viva" o "célula muerta" durante diversas generaciones en el modelo "Juego de la vida" de John Conway.

muestra la dinámica que siguen las celdas hasta la cuarta generación. ¿Puede el lector predecir qué celdas estarán vivas o muertas para la quinta generación?

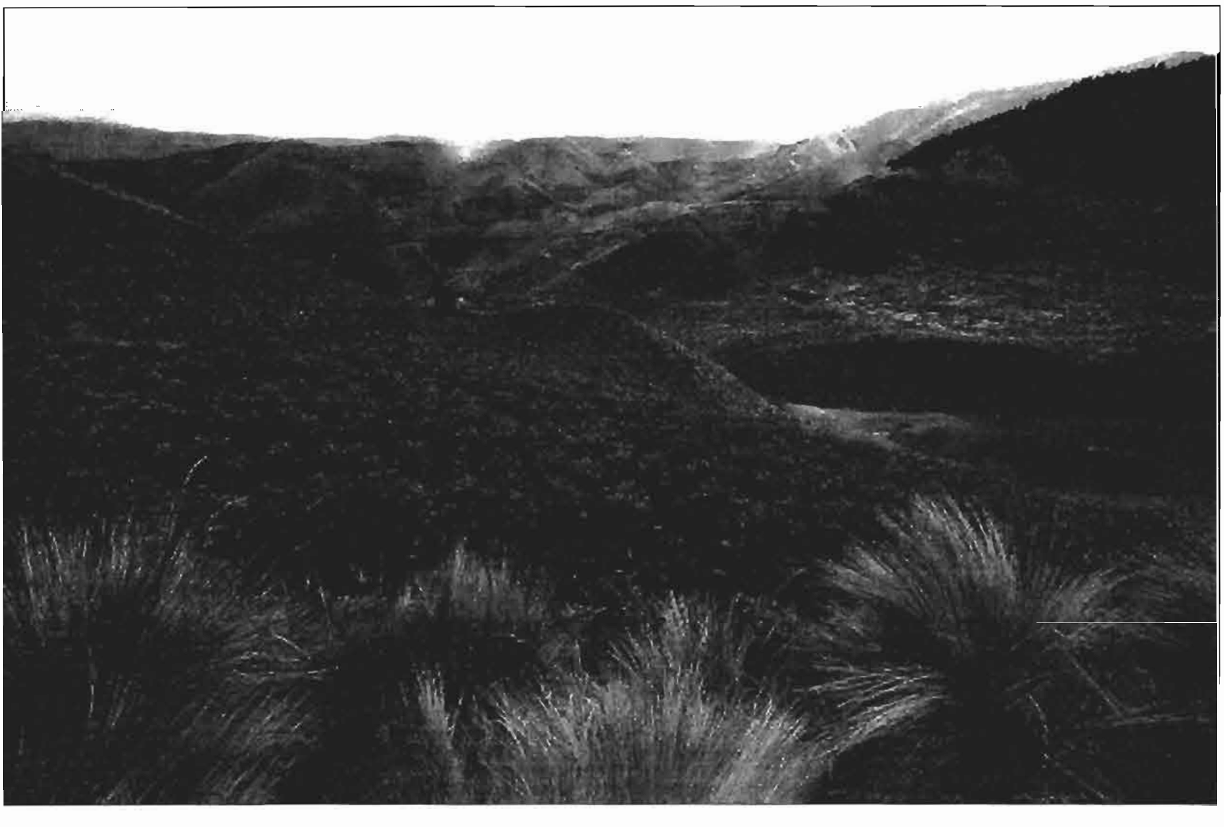
Un autómata celular para simular la dinámica de una plaga invasora en el Ecuador

Un claro ejemplo de plaga invasora es la Polilla Guatemalteca de la Papa *Tecia solanivora*, un pequeño lepidóptero de la familia Gelechiidae cuyas larvas atacan exclusivamente a los tubérculos de la papa tanto en los campos cultivados como en las bodegas. *T. solanivora* ha estado invadiendo exitosamente la zona norte de los Andes durante los últimos 30 años. Llegó a nuestro país desde Colombia en 1996 a causa de intercambios comerciales en la frontera entre los dos países. Junto con otras dos especies de polillas de papa, *Phthorimaea operculella* y *Symmetrischema tangolias*, *T. solanivora* es considerada como una de las mayores plagas de papas en Centro América y el norte de Sur América. Diversos estudios han comprobado que la infestación es comúnmente más alta en las bodegas donde se almacenan los tubérculos ya que éstas presentan condiciones óptimas para el desarrollo de las polillas, como protección contra temperaturas extremas o contra las precipitaciones que normalmente afectan el desarrollo, la supervivencia y la fecundidad de estos insectos.

Los Andes, gracias a que encierran gran cantidad de zonas remotas y aisladas, son una región ideal para el estudio de invasiones biológicas. Su alta heterogeneidad limita la dispersión natural de las especies. En este contexto, cambios ambientales causados por el hombre, como la construcción de vías, adquieren gran importancia para la dispersión de organismos, especialmente aquellos de vuelo limitado como las polillas de la papa (Fig. 2). Mecanismos pasivos de transporte a grandes distancias, como por ejemplo en vehículos humanos transportando papas desde cultivos a mercados o entre poblaciones humanas, son probablemente, los medios por los cuales estos insectos invaden nuevos sitios.

Con el fin de entender, predecir y avanzar en el control de la propagación de la Polilla Guatemalteca, el Laboratorio de Entomología de la PUCE, con apoyo de la Fundación McKnight y del IRD (Institute de Recherche pour le Développement), está actualmente desarrollando un modelo autómata celular llamado **SimPolilla.**

Estamos inicialmente probando el modelo en el valle de Simiatug, localizado en la provincia de Bolívar, en el cantón Guaranda. Este



Por Olivier Dangles

Figura 2. Los transportes de las polillas por los seres humanos pueden ayudar a la plaga a colonizar los cultivos (por ejemplo de papa) a mayor altura, en zona de frontera agrícola.

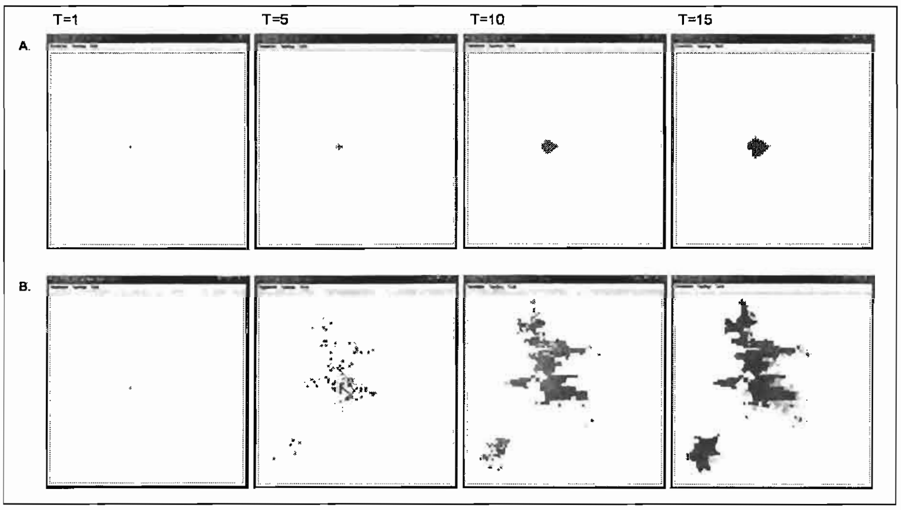


Figura 3. Simulación de la propagación de la polilla en el valle de Simiatug durante 15 generaciones. A) Sólo se toma en cuenta la dispersión a cortas distancias por difusión (sin intervención del hombre); B) interviene también la dispersión pasiva a grandes distancias en vehículos humanos. Observamos como en B la propagación no sólo es más rápida sino que también los insectos son capaces de "saltar" a celdas alejadas.

valle constituye un ejemplo primordial para estudiar la expansión de *T. solanivora* ya que sabemos que la propagación de la polilla inició en el año 2006 con la rehabilitación de la carretera de Salinas a Guaranda y el consecuente movimiento de productos de y hacia el valle. El monitoreo de polillas adultas en el valle desde el año 2006 nos permitirá comparar y validar las predicciones de nuestro modelo. Como en todos los autómatas celulares, el área de estudio se debe dividir. En el caso de **SimPolilla** se divide en celdas de 0,25km^2. Cada celda está definida por variables de estado como la elevación, la temperatura y la precipitación medias mensuales, el uso de suelo y la abundancia de polillas inmaduras (huevos, larvas y pupas), adultas y hembras grávidas. Las reglas que regulan la dinámica de las polillas en y entre las celdas se basan en respuestas fisiológicas de las polillas a las variables geográficas. Por ejemplo, sabemos que la supervivencia de las polillas se relaciona de manera no linear con la temperatura, con un rango óptimo de temperaturas y con umbrales a altas y bajas temperaturas. De esta manera nuestro modelo calcula la tasa de supervivencia de los insectos en cada celda de acuerdo a su temperatura. Otros aspectos de la dinámica de las polillas, como la tasa de desarrollo, la reproducción y la dispersión pasiva (sin intervención del hombre) entre celdas vecinas son también simuladas por el modelo (Fig. 3A).

Debido a la gran importancia del hombre en la dinámica de la expansión de la polilla quisimos integrar ciertas prácticas humanas, como la presencia de bodegas de papas, el manejo de la plaga (ej. uso de plaguicidas) y la dispersión a grandes distancias en vehículos humanos (Fig. 3B), en nuestro modelo.

Así podremos comparar la propagación de la plaga con o sin la intervención del hombre y vislumbrar hasta qué punto el hombre es responsable de la invasión de la polilla de la papa a nuevos territorios. El modelo servirá además, como herramienta de capacitación para concientizar a los agricultores sobre la importancia de un manejo adecuado de sus cultivos para frenar la expansión de esta plaga (Fig. 4).


Por Perrine Garassus

Figura. 4. Fotografía de una capacitación a campesinos de varias comunidades Quechuas en el valle de Simiatug, en la que se utilizó nuestro modelo para demostrar los peligros de infestación con un manejo inadecuado de la plaga.

Literatura consultada

Baltzer, H., Braun, P.W., Kohler, W. 1998. Cellular automata models for vegetation dynamics. Ecological Modelling 107:113–125.

Liebhold, A.M. and Tobin P.C. 2008. Population Ecology of Insect Invasions and Their Management. Annual Reviews of Entomoly 53:387–408.

Mooney, H., and Hobbs, R. J. 2000. Invasive species in a changing world. Island Press, Washington, D.C., USA.

Neumann , J.von. 1966. Theory of self-reproducing Automata. University of Illinois Press. Urbana, Illinois, USA. 388 pp.