Modélisation de la dynamique spatio-temporelle d'insectes ravageurs des cultures dans des systèmes socio-écologiques

François Rebaudo

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L'UNIVERSITE PIERRE ET MARIE CURIE

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(Ecole doctorale Diversité du Vivant)

Présentée par

M. François REBAUDO

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Sujet de la thèse :
Modélisation de la dynamique spatio-temporelle d'insectes ravageurs des cultures dans des systèmes socio-écologiques

Soutenue le 17 juillet 2012 devant le jury composé de :

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- **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. ***Journal of Artificial Societies and Social Simulation*** 14:3.

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- **Rebaudo F.**, Crespo-Pérez V., Silvain JF., Dangles O. (2010) Intégrer les interactions interspécifiques dans la modélisation de la dynamique de la biodiversité, le cas de ravageurs des cultures en Équateur. ***11th Orsay's pluridisciplinairy conference "Biodiversité : de la Molécule à l'Ecosystème"***, Orsay, France, Mars 2010. *Distingué par un prix du jury.*

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Modélisation de la dynamique spatio-temporelle d'insectes ravageurs des cultures dans des systèmes socio-écologiques

Résumé

Les systèmes socio-écologiques sont omniprésents et la compréhension de leur fonctionnement est devenue une priorité pour aborder de manière commune et précise les questions soulevées par l'action de l'homme sur son environnement, mais aussi pour identifier des trajectoires et explorer des scénarios prospectifs sur la base desquels, une stratégie de pilotage pourrait être envisagée. Appliquée à un ravageur des cultures dans le nord des Andes, l'approche de ces systèmes par un modèle d'automate cellulaire a permis d'identifier les facteurs humains clefs de sa dispersion et de disposer de cartes de probabilité de présence. Par la suite, l'intégration de variabilité génétique par un modèle individu-centré a facilité l'exploration de scénarios de structuration des populations de ravageurs. Pour une meilleure compréhension de la dynamique spatio-temporelle de ces derniers, une approche à base d'agents, théorique puis empirique, a fourni des éléments d'explication des délais observables entre la mise au point d'une technique de protection des cultures et son application par les agriculteurs d'une petite région agricole, par un modèle de diffusion de l'information couplé aux approches précédentes. Afin d'exploiter ces résultats et suite à une recherche participative fructueuse dans la zone d'étude, une méthode innovante basée sur un modèle a été insérée dans un programme de formation d'agriculteurs pour souligner la nécessité d'une approche systémique pour une protection des cultures efficace. Malgré certaines limitations, ces approches pourraient être applicables plus largement à tout programme agricole dans des systèmes socio-écologiques.

Mots clefs :
modèles ; simulation ; ravageurs des cultures ; systèmes complexes ; systèmes socio-écologiques ; paysage

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Spatio-temporal modeling of pests dynamics in social-ecological systems

Abstract

Social-ecological systems are omnipresent and the understanding of their functioning became a priority not only to approach in a common and precise way the questions raised by the action of human on its environment, but also to identify trajectories and investigate forward-looking scenarios on the basis of which, management strategies could be developed. Applied to a crop pest in the Northern Andes, a cellular automaton approach allowed us to identify key human factors of pest dispersal and to construct maps from presence/absence probability. Afterward, the integration of genetic variability through an individual-based model facilitated the exploration of pest populations structure scenarios. For a better understanding of pest spatio-temporal dynamics, an agent-based model approach, theoretical then empirical, supplied elements of explanation of observable delays between the development of a crop protection innovation and its application by farmers of a small agricultural region, through an information diffusion model coupled with the previous approaches. To further exploit these results after a fruitful participative research in the study zone, an innovative method based on a model was fitted into a farmers' training program to underline the necessity of a systematic approach for an effective integrated pest management program. Despite some limitations, these approaches could be applicable more widely to any agricultural program in social-ecological systems.

Key words:
models ; simulation ; pests ; complex systems ; social-ecological systems ; landscape

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INTRODUCTION

Introduction

1. Systèmes complexes et complexité des systèmes

1.1. Définitions

La complexité est partout, associée à l'histoire (Hunt et Lipo 2011), la politique (Geyer et Rihani 2010), l'art (Boon *et al.* 2011), l'informatique (Blakey 2011) ou la gastronomie (This 2009). Elle fait tout autant la une des journaux (Schieb 2011 ; Sussan 2011) que l'objet d'essais (Norman 2011), et ce pour une raison très simple : nous vivons dans un monde complexe, *i.e.* composé de plusieurs parties ou éléments interconnectés (dictionnaire Larousse Éditions 2009). Au sein de la communauté scientifique, la complexité revêt donc naturellement un caractère transdisciplinaire (en attestent les conférences[2] et les revues scientifiques[3] qui lui sont consacrées). Pour autant la complexité d'un système (*i.e.* d'un ensemble cohérent) en fait-elle un système complexe ? S'il n'existe pas de consensus quant à la notion de système complexe au sein de la communauté scientifique (Varenne 2009), il est cependant généralement admis qu'il se caractérise par un système composé d'entités en interaction, dont la complexité viendrait des types d'interaction et/ou des types de résultats issus de ces interactions (Varenne 2009). En accord avec Simon (1976), qui définit les types d'interaction comme une des mesures de la complexité, c'est donc par les résultats issus des interactions entre entités que sera défini, dans ce manuscrit, un système complexe. Par entité, du latin *ens, entis* (étant), le dictionnaire Larousse (dictionnaire Larousse Éditions 2009) propose notamment « *une chose considérée comme un être ayant son individualité : la société, l'état sont des entités* ». En informatique, l'entité est une structure composée d'attributs, ou encore la composante (élément) d'un système fonctionnel. Elle est utilisée dans les modèles de données entité-association (« *entity-relationship models* », Chen 1976, Pinet 2012) permettant de décrire les modèles conceptuels de données. Un système complexe serait donc un ensemble cohérent d'éléments composés d'attributs, ces éléments étant en interactions et générant des résultats particuliers (voir Fig. 1). Parmi les résultats générés, pour qualifier la catégorie de résultats caractérisant un système complexe, nous ferons

[2] *e.g. International Conference on Complex Systems* ; *International Conference on Complex Systems and Applications* ; *European Conference on Complex Systems* ; *Conférence Modélisation Mathématique et Informatique des Systèmes Complexes* ; *Complex Systems Design & Management Conference*.

[3] *e.g. Ecological Complexity*, *Journal of Complexity*, *Reviews of Nonlinear Dynamics and Complexity*, *Computational Complexity*, *Journal of Social Complexity*, *Complexity*, *Bio-Complexity*, *Chaos and Complexity*.

référence, dans ce manuscrit, au concept d'émergence[4]. La citation qui serait attribuée à Aristote d'après l'ouvrage Métaphysique publié après sa mort (livre H, vers 60 av. J.-C.) : « *la totalité est plus que la somme des parties* » est un exemple de définition[5]. Dans cette dernière, « plus » n'est pas nécessairement à comprendre quantitativement, mais plutôt comme « autre chose », qui peut être temporel, spatial ou encore fonctionnel. Dans ce manuscrit, la définition proposée par l'auteur d'un système complexe serait la suivante :

> *« Un système complexe est un ensemble cohérent composé d'entités en interactions, dont en résultent des propriétés spatiales, temporelles ou fonctionnelles émergentes. »*

Si les propriétés émergentes d'un système complexe ne sont peu ou pas déductibles d'après les entités qui le composent, cela signifie qu'elles ne peuvent être prédites (Hosseinie et Mahzoon 2011). Une possibilité consiste à observer le système pour pouvoir suivre l'évolution des entités, de leurs attributs et interactions. Outre l'observation, pour identifier des scénarios possibles d'évolution du système, une alternative consiste à représenter le système de manière simplifiée, *i.e.* à le modéliser (Sitte 2009).

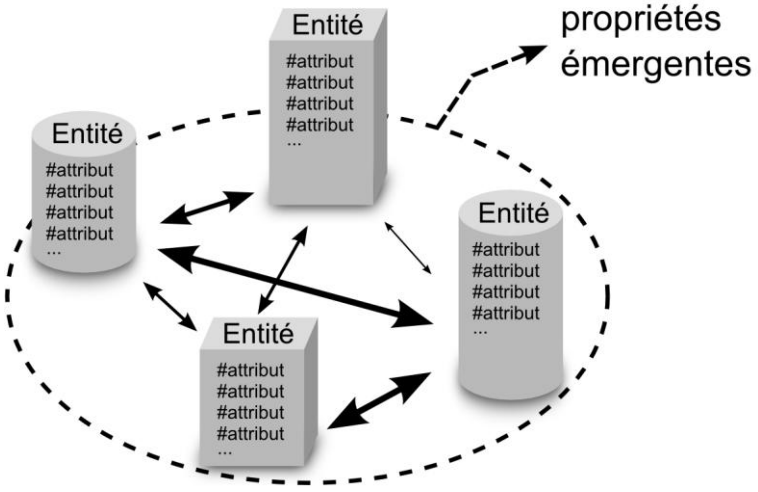

Fig. 1 : Représentation d'un système complexe avec des entités hétérogènes aux interactions variées conduisant à des propriétés émergentes

[4] Tous les résultats d'un système complexe ne sont pas nécessairement émergents. En ce sens l'émergence correspond à une catégorie de résultats.

[5] Il n'existe pas de consensus au sein de la communauté scientifique quant à la définition de l'émergence. La définition proposée dans ce manuscrit se base sur les travaux de Corning (2002).

1.2. La modélisation des systèmes complexes

Un modèle est une représentation simplifiée d'un système (Boccara 2004). Toutes les entités et leurs interactions ne sont donc pas représentées, introduisant ainsi un niveau d'abstraction (Sitte 2009). De manière générale, un modèle est construit pour poursuivre un objectif donné, et son usage à d'autres fins peut conduire à des interprétations erronées (Bonabeau 2002). Les objectifs peuvent être variés, depuis la compréhension d'un processus jusqu'à son usage comme support de travail interdisciplinaire, en passant par la scénarisation prospective (voir Epstein 2008 pour une discussion sur les usages des modèles). Il doit donc contenir, comme indiqué ci-après, le niveau de détail adapté à son objectif. A titre d'exemple, pour modéliser le flux de voitures dans l'objectif de comprendre la formation d'embouteillages, les voitures peuvent être représentées de manière abstraite par des flèches pointant la direction du véhicule (voir l'article de référence de Biham *et al.* 1992). Si les relations qui le composent sont suffisamment simples, une solution analytique peut être trouvée *via* des méthodes mathématiques, mais dans de nombreux cas, la simulation numérique est nécessaire (Law et Kelton 2000). Pour cette dernière, la représentation du système est dynamique (*i.e.* avec des changements d'état dans le temps et/ou l'espace). La simulation doit cependant bien être distinguée du réel car elle conduit à un scénario dans un contexte particulier, plus ou moins probable en fonction du modèle utilisé (voir Conroy *et al.* 1995). C'est donc un outil de scénarisation ou de prévision dans un contexte donné (*i.e.* imaginer ce qui pourrait se passer), et non de prédiction (*i.e.* annoncer ce qui va arriver). Cette distinction est d'autant plus importante dans le contexte actuel où l'on retrouve de plus en plus, associé à un scénario ou groupe de scénarios prospectifs, une probabilité d'occurrence ou un indice de fiabilité (*e.g.* scénarios IPCC du changement climatique, voir Fig. 2), dans un contexte d'évolution donné.

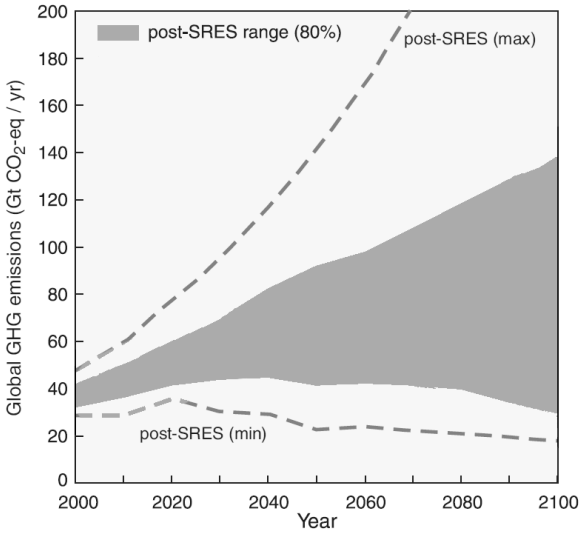

Fig. 2 : Scenarios des émissions de gaz à effet de serre de 2000 à 2100 sous l'hypothèse d'une conservation des politiques climatiques actuelles. La fiabilité des scénarios est représentée par l'aire grisée avec les scenarios extrêmes en pointillés (d'après IPCC Climate Change 2007).

Pour simuler un système complexe, en intégrant explicitement les entités considérées, l'approche mécaniste de type ascendante est toute indiquée (de l'anglais « *bottom-up* », par opposition à l'approche de type descendante, de l'anglais « *top-down* »). La démarche est alors descriptive: identification des entités, de leurs attributs, des échelles spatiales et temporelles, ainsi que des interactions (voir Amouroux 2011 pour une révision des méthodes de modélisation descriptives des systèmes complexes et du cycle de modélisation). La représentation du système peut ainsi être construite conjointement avec les différents acteurs concernés (scientifiques, porteurs d'enjeux), avec un niveau d'abstraction adapté à la question initiale (Sitte 2009). La résultante de ce niveau d'abstraction est qu'il existe des modèles simples de système complexe comme des modèles complexes de système complexe. Kotiadis et Robinson (2008) soulignent ainsi l'importance de la consultation des acteurs dans le choix du niveau d'abstraction, tout en rappelant les avantages des modèles simples : i) leur développement est plus rapide (y compris la vérification et la validation), ii) ils sont plus flexibles, iii) ils nécessitent moins de données, iv) leurs résultats sont plus faciles à interpréter et v) ils améliorent la transparence (communication et appropriation). Pour Edmonds et Moss (2005), l'approche doit avant tout rester descriptive. Dans celle-ci, la simplification s'opère *a posteriori*, contrairement à l'approche traditionnelle visant à incrémenter la complexité des modèles jusqu'à expliquer les données observées (*e.g.* la régression itérative pas-à-pas de type

« *stepwise* »). Pour Bonabeau (2002), le choix du niveau d'abstraction pour un objectif donné est plus un art qu'une science[6], et pour Drogoul (2010), il s'agit d'une stratégie.

A titre d'illustration, un exemple célèbre de modèle simple d'un système complexe est le jeu de la vie imaginé en 1970 par John H. Conway, alors professeur à l'Université de Cambridge (Fig. 3). Ce jeu est constitué d'une grille à deux dimensions formant un ensemble de cellules, chaque cellule pouvant prendre deux états : vivante ou morte. L'évolution d'une cellule est ensuite déterminée en fonction de l'état des huit cellules voisines (voisinage de Moore), par les règles suivantes appliquées simultanément à toutes les cellules :

- Une cellule morte, possédant exactement trois voisines vivantes, devient vivante.
- Une cellule vivante, possédant deux ou trois voisines vivantes, reste vivante, sinon meurt.

En dépit de la simplicité des règles, une population évoluant ainsi manifeste un nombre important de structures spatiales et temporelles émergentes (voir Bak *et al.* 1989).

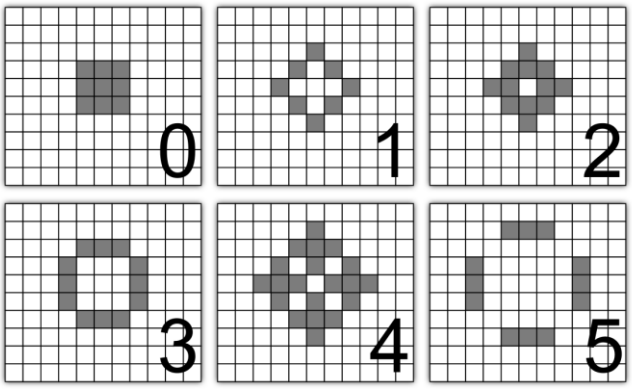

Fig. 3 : Jeu de la vie sur une grille de 11 par 10 cellules avec un carré de trois sur trois cellules vivantes à l'instant t=0 simulé pendant 5 générations. Les cellules vivantes sont représentées en gris et les cellules mortes en blanc (Gardner, 1970).

Il s'agit toutefois de garder à l'esprit que les notions de simplicité et de complexité sont relatives (la comparaison de deux modèles complexes permet d'identifier un modèle comme plus « simple » que l'autre), et que au-delà de leur caractérisation, c'est la pertinence de la complexité d'un modèle pour un objectif donné, qui importe.

1.3. Types de modèles

Dans un système complexe, les entités qui le composent peuvent être hétérogènes (voir Fig. 1), et distribuées spatialement de manière explicite (voir Fig. 3). Cette hétérogénéité fonctionnelle et spatiale peut être à l'origine de dynamiques non-linéaires, de seuils ou de

[6] « *The model has to be built at the right level of description, with just the right amount of detail to serve its purpose; this remains an art more than a science.* »

boucles de rétroaction (Liu *et al.* 2010). Pour sa représentation, les systèmes d'équations différentielles (même partielles pour la prise en compte de l'espace), ou encore les modèles statistiques, ne peuvent être employées pour représenter le système dans son ensemble, car dans ces derniers, ce sont des moyennes (ou des fonctions lissées) qui sont représentées et non des entités individuelles et autonomes (Boccara 2004). L'alternative est le recours aux modèles de type automates cellulaires, individus-centrés et agents-centrés (Bonabeau 2002). Cette alternative consiste à décrire le système à partir des éléments qui le compose (approche ascendante, voir plus haut), et ne s'oppose pas pour autant aux approches précitées. En effet, un jeu d'équations différentielles peut par exemple définir la dynamique de chaque entité du système (Bonabeau 2002).

Automates cellulaires : Un automate cellulaire (AC) est une grille (ou tout autre type de structure spatiale) de dimension *d* constituée d'entités identiques pouvant prendre un nombre d'états finis susceptibles d'évoluer dans le temps (système dynamique discret), en fonction de règles de transition (*i.e.* règles spécifiant l'état que va prendre une entité à la génération suivante en fonction de son état et de l'état des entités voisines, identiques pour toutes les entités) (Daudé 2003). Le jeu de la vie présenté précédemment est un automate cellulaire à deux dimensions où les entités sont des cellules (voir Fig. 3). Dans la pratique, un AC peut être étendu à la manière d'un système d'information géoréférencé (Li et Yeh 2000). Dans ce dernier, l'information est représentée sous forme de couches, et chaque entité peut prendre un ensemble de valeurs pouvant être discrètes ou continues (voir Fig. 4). Les règles de transition introduites dans ces couches peuvent alors être différentes (non liées aux valeurs des entités voisines, *e.g.* la température qui varie dans le temps, la taille de la végétation qui varie en fonction de la qualité du sol). De part l'émergence de propriétés issues des interactions locales, les AC sont un outil privilégié dans l'étude des systèmes complexes (Wolfram 1984). Ils sont particulièrement utilisés pour reproduire avec réalisme des patrons spatiaux occupant une place importante dans le système représenté (usage du sol, urbanisation, voir Parker *et al.* 2003, Matthews *et al.* 2007, Guan *et al.* 2011). Cependant, lorsque des entités mobiles ou des comportements doivent être introduits, les AC sont subtilisés ou utilisés de manière couplée avec des systèmes multi-agents[7] (Epstein et Axtell 1996).

[7] Dans ce manuscrit, en accord avec Daudé (2003) et Ferber (1995, lire le paragraphe 4.6.3. p190 pour discussion), les automates cellulaires ne sont pas considérés comme des systèmes multi-agents car les entités

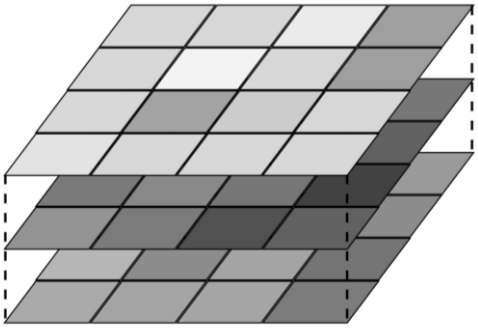

Fig. 4 : Représentation d'un automate cellulaire à *d* = deux dimensions (4*4 entités) avec trois types d'état par entité (trois couches pour l'utilisation de trois informations différentes).

Systèmes multi-agents : un système multi-agents (SMA), est un modèle composé d'entités autonomes pouvant agir sur elles-mêmes et sur leur environnement (Daudé 2003). Historiquement, lorsque l'objectif du modèle porte majoritairement sur les interactions locales et la variabilité individuelle des entités, les modèles sont dits « individu-centrés », et lorsqu'il porte sur les décisions et les comportements d'adaptation des entités, les modèles sont dits « agent-centrés » ou « à base d'agents » (Railsback et Grimm 2011). Un exemple célèbre de modèle agent-centré est celui de Helbing *et al.* (2000), représentant le comportement d'une foule en panique évacuant une salle en feu (voir Fig. 5). Dans cet exemple, la vitesse à laquelle les individus (passants) sortent de la salle et le nombre d'individus blessés dans un contexte de panique, sont des propriétés émergentes du système, permettant d'établir et d'évaluer des scénarios d'évacuation. Ici les relations entre les passants et l'environnement sont simples, ce dernier n'étant constitué que de murs et d'espaces ouverts, tous deux statiques. Les passants sont quant à eux caractérisés par leur corpulence, leur vitesse, et le respect d'une distance entre eux en fonction des caractéristiques de l'environnement (la vitesse et le respect d'une distance entre passant changent en fonction de stimuli externes comme un départ d'incendie dans la salle). Ce type de modèle peut générer des résultats contre intuitifs, comme démontré par Helbing *et al.* (2000) : une colonne placée devant l'issue de secours et légèrement excentrée permet ainsi d'augmenter le flux de sortie des passants et de réduire le nombre de blessés (voir Fig. 5B).

autonomes ne peuvent pas se déplacer. D'autres auteurs, comme Boccara (2004), les considèrent comme des systèmes multi-agents où les agents sont fixes.

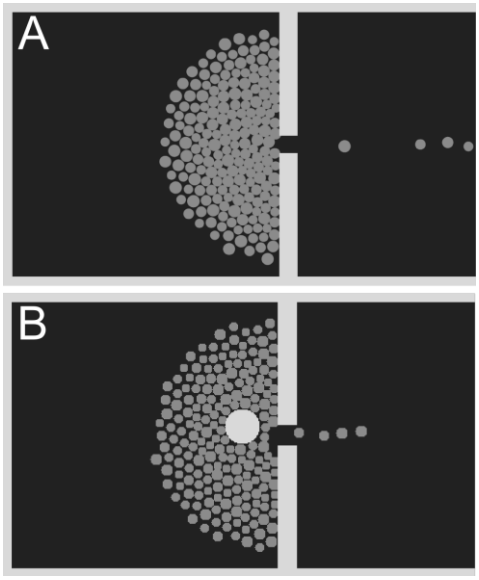

Fig. 5 : Simulation agent-centrée de passants représentés par des ronds gris de différentes tailles se déplaçant vers la sortie de la salle. En A, aucun aménagement de l'espace n'est inclus (vitesse d'évacuation faible et nombre de blessés importants) et en B, une colonne est placée devant la sortie de manière légèrement excentrée pour optimiser le flux de sortie des passants (vitesse d'évacuation plus rapide et nombre de blessés réduit). Ces travaux ont contribué au développement de systèmes d'évacuation de bâtiments, mais aussi à une meilleure compréhension des comportements de foule (d'après Helbing *et al.* 2000).

Cependant, dans la plupart des systèmes, la compréhension des relations dynamiques et non-linéaires entre les humains et leur environnement constitue un challenge scientifique majeur (Murray-Rust *et al.* 2011). Dans « *les voies à suivre pour les modèles et les scénarios de biodiversité* », la Convention sur Diversité Biologique (2010) identifie par exemple une série de facteurs importants et manquants dans les modèles, dont la surexploitation des systèmes, la dégradation des habitats ou encore les espèces envahissantes, ainsi que le manque de relations générales et évolutives entre ces facteurs et les changements observés dans la nature. Malgré le consensus sur l'importance de l'incorporation des services écosystémiques dans la gestion des ressources naturelles, leur quantification reste difficile (Nelson *et al.* 2009), comme par exemple dans le cas des systèmes agricoles. De part la nature descriptive de leur approche, les SMA semblent tout indiqués pour répondre à ces challenges (Matthews *et al.* 2007).

2. Les systèmes agricoles, des systèmes socio-écologiques complexes

2.1. Les systèmes socio-écologiques

Nous vivons sur une planète dominée par l'homme où les changements que nous opérons sont plus rapides que notre capacité à en comprendre les conséquences (Vitousek *et*

al. 1997). Pour étudier la résilience, la vulnérabilité et l'adaptation des systèmes que l'homme a artificialisé, les études sociales et écologiques ont évolué vers une approche couplée, l'étude des systèmes socio-écologiques (Young *et al.* 2006 et Fig. 6). Les systèmes socio-écologiques (SES) sont des systèmes dans lesquels interagissent un ou plusieurs systèmes écologiques avec un ou plusieurs systèmes sociaux, traitant ainsi d'entités écologiques (*e.g.* biodiversité, patrons du paysage), d'entités sociales (*e.g.* réseaux sociaux, gouvernance), mais aussi d'interactions liant les aspects environnementaux et humains (*e.g.* consommation des ressources et autres services écosystémiques) (Liu *et al.* 2007).

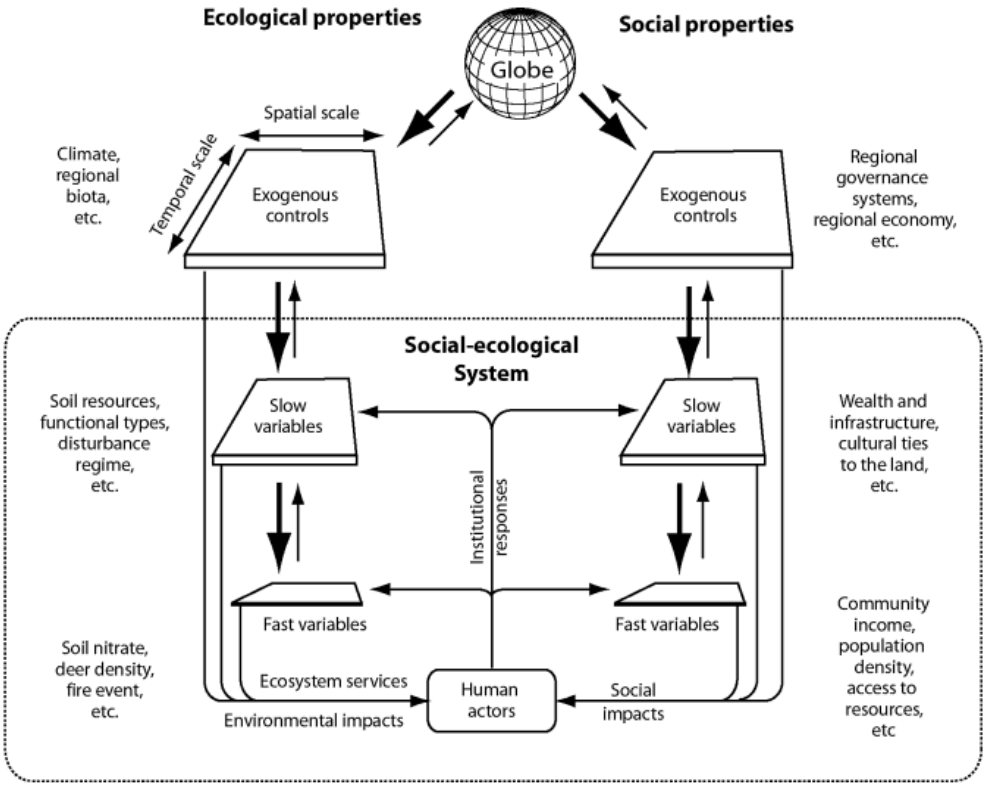

Fig. 6 : Diagramme d'un système socio-écologique (ou « Coupled Human And Natural Systems » CHANS, voir Liu *et al.* 2007), affecté par des propriétés écologiques à gauche et sociales à droite (d'après Chapin *et al.* 2009).

Ces systèmes se caractérisent notamment par une dynamique non linéaire avec des seuils, des boucles de rétroaction ou des décalages dans le temps (Liu *et al.* 2007), et sont donc susceptibles de changer de manière inattendue (Chapin *et al.* 2009). Dans leur étude socio-écologique des réserves marines, Pollnac *et al.* (2010) montrent par exemple que l'état des stocks de poissons est le résultat d'interactions sociales complexes plutôt qu'une simple réponse au renforcement des règles de gestion.

Dans un contexte de transdisciplinarité des approches scientifiques, l'étude des systèmes socio-écologiques est de plus en plus plébiscitée, particulièrement via les systèmes multi-agents, qui permettent de mobiliser de manière réaliste les connaissances en sciences humaines et sociales (Smajgl *et al.* 2011). Cette caractéristique, ajoutée aux propriétés émergentes et à la non-adéquation des approches de modélisation disponibles jusqu'à présent, font des SMA un développement considéré comme majeur en sciences sociales, dont le potentiel reste à exploiter (Hamill 2010, Bankes 2002). Dans sa révision de littérature des modèles agents-centrés des SES, An (2011) souligne l'importance de la modélisation des processus décisionnels, mais aussi l'usage couplé avec des automates cellulaires, pour représenter explicitement le paysage. Outre la gestion des réserves marines, ces applications sont nombreuses pour les études d'usage du sol (voir Matthews *et al.* 2007), la gestion de ressources et la biologie de la conservation (voir Bousquet et Le Page 2004), et de plus en plus présentes pour l'agriculture et les systèmes agricoles (Schreinemachers et Berger 2011).

2.2. Particularités des paysages agricoles

Dans la plupart des pays du monde, la terre est essentiellement utilisée à des fins agricoles, si bien que l'agriculture joue un rôle majeur dans le modelage des paysages (Firbank *et al.* 2008, Ziegler *et al.* 2011,). Ces paysages constituent des systèmes socio-écologiques, où l'environnement et les activités humaines sont étroitement liées (Hufnagl-Eichiner *et al.* 2011, et Fig. 7). Dans ces SES, les spécificités majeures sont i) un découpage de l'espace sous forme de parcelles (avec ou sans zones adjacentes non exploitées), ii) une rotation dans le temps des couverts végétaux (avec des cycles courts et des cycles longs), iii) une exploitation des ressources (de l'extensif à l'intensif), et iv) une sélection négative des espèces portant atteinte à la productivité (Petit 2009). Les paysages agricoles forment donc une mosaïque dynamique de patches variant dans leur taille, leur forme et leur disposition, résultat d'interactions entre des éléments physiques (*e.g.* climat, qualité du sol), biologiques (*e.g.* populations de ravageurs, variétés de cultures) et sociaux (*e.g.* comportements individuels et collectifs d'agriculteurs) (Petit 2009). De ce fait ils sont hétérogènes dans l'espace, dans le temps, mais aussi dans les pratiques des agriculteurs (Beyene *et al.* 2006, Kiba *et al.* 2012).

Fig. 7 : Paysage agricole dans les Andes Equatoriennes (Province de Carchi, 3300 m). Au premier plan à droite un champ de pomme de terre est inclus dans une matrice d'habitats hétérogènes et artificialisés à plusieurs degrés (prairies, bois, haies, vallées, collines, villages). Au centre, un agriculteur est en interaction avec le système (en l'occurrence la culture en place et les communautés d'insectes associées) via l'application d'un traitement insecticide (photo O. Dangles).

2.3. Protection des cultures et stratégies de lutte

Dans un contexte d'augmentation de la population humaine et donc de la demande en nourriture (Tilman *et al.* 2011), la protection des cultures (ici limitée à la lutte contre les ennemis des cultures) tient un rôle clef en combattant les adventices, les ravageurs, les pathogènes et les virus (Oerke et Dehne 2004). Ils représentent en effet la cause majeure des pertes de récolte (de l'ordre de 30% pour les grandes cultures, voir Birch *et al.* 2011). La protection des cultures permet ainsi de préserver le potentiel de production, mais aussi de régulariser les rendements et d'assurer la qualité des denrées alimentaires (Oerke et Dehne 2004). Les méthodes de lutte pour faire face à ces menaces sont nombreuses (choix des variétés, mesures prophylactiques, lutte chimique, lutte biologique, etc), en fonction de la stratégie de lutte considérée. La protection intégrée des cultures, (« *integrated pest management* » aux Etats Unis ou « *integrated crop protection* » en Grande Bretagne), telle que définie par l'Internationale de Lutte Biologique et intégrée contre les animaux et les plantes nuisibles (OILB) et la Section Régionale Ouest Paléarctique (SROP) en 1973 (voir Ferron 1999), constitue un « *système de lutte contre les organismes nuisibles qui utilise un ensemble de méthodes satisfaisant les exigences à la fois économiques, écologiques et toxicologiques, en réservant la priorité à la mise en œuvre délibérée des éléments naturels de limitation et en respectant les seuils de tolérance* ». Cette approche écologique de la régulation des populations d'organismes nuisibles aux cultures considère de ce fait l'agro-écosystème (dans sa définition en tant que système socio-écologique agricole) pour la définition des actions de lutte à mener (Ferron 1999). Cela suppose de comprendre le

fonctionnement des SES, en particulier les interactions entre le système physique et écologique et les activités humaines et de ce fait, les processus qui conduisent aux décisions humaines (Smajgl *et al.* 2011). Par exemple, la décision d'un agriculteur quant à l'adoption d'une innovation agricole pourra être basée sur l'intérêt que celle-ci présente compte tenu de sa disponibilité, des usages de ses voisins, de l'état de ses sols, ou encore de ses expériences passées, entre autres facteurs sociaux et économiques (Berger 2001). La prise en compte du comportement des agriculteurs reste cependant un défi majeur, car les décisions humaines et les actions qui en découlent ont un effet direct sur la structure et les fonctions des systèmes agricoles (An 2011). Elles sont en tout état de cause le résultat d'un choix stratégique au sein des alternatives possibles (Montanari et Saberi 2010, Feola et Binder 2010). Pour reprendre l'exemple d'une innovation agricole, basé sur la théorie de Rogers (1962) de diffusion et d'adoption d'un nouveau produit, le modèle de Bass (1969) est traditionnellement utilisé pour évaluer le nombre de nouveaux adoptants en fonction du temps (voir Fig. 8). Ce dernier ne prend cependant pas en compte l'hétérogénéité des populations qui peut conduire à des résultats très différents (Bonabeau 2002). Dans ce cadre, la modélisation agent-centrée apparaît comme tout indiquée pour construire des scénarios (Montanari et Saberi 2010), par rapport aux approches traditionnelles (voir la comparaison de Kuandykov et Sokolov 2010 entre modèles agent-centrés et autres approches).

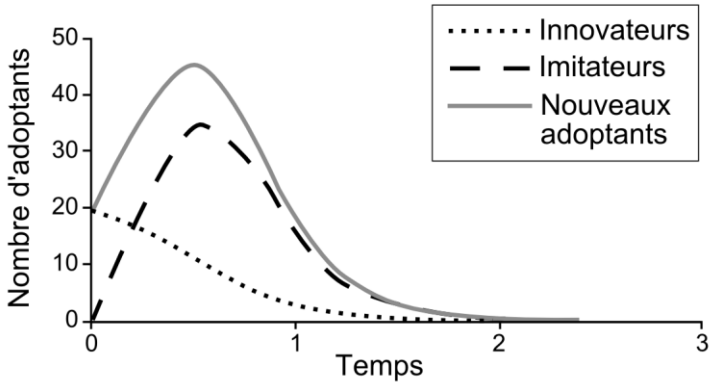

Fig. 8 : Représentation de la diffusion d'une innovation selon le modèle de diffusion de Bass (1969).

Cela est d'autant plus vrai dans le cas des menaces agricoles (par exemple des insectes ravageurs), où les aspects spatiaux et temporels influencent fortement les décisions des agriculteurs. En effet, la plupart des facteurs d'occurrence d'une menace sont liés à leur déplacement propre ou aux pratiques des agriculteurs voisins, passées ou présentes (Veres *et al.* 2011). Epanchin-Niell *et al.* (2010) décrivent ainsi l'abandon par les agriculteurs de la lutte contre un adventice envahissant à cause de la ré-infestation continue provenant des

autres acteurs du paysage (routes, lieux publics, zones résidentielles). De l'échelle de l'exploitation ou de la parcelle, la stratégie de lutte intégrée passe à l'échelle du paysage. Ce constat s'applique particulièrement dans le cas d'un type de menace particulier, les ravageurs des cultures.

3. Insectes ravageurs des cultures et modélisation

3.1. Insectes ravageurs des cultures

Les insectes ravageurs des cultures sont des insectes nuisibles pour les cultures agricoles, constituant une menace majeure pour la production de denrées alimentaires (Birch *et al.* 2011). Les préjudices causés peuvent être directs, par l'alimentation des insectes (voir Fig. 9) ou indirectes via la transmission de virus, les excrétions (*e.g.* miellats des pucerons provoquant la formation de fumagine), ou encore la réaction des plantes (*e.g.* galles). Ils sont très variés, la base encyclopédique HYPPZ (Fraval *et al.* 1997) regroupant par exemple près de 300 fiches (espèces) décrivant les ravageurs importants dans la seule Europe occidentale (la base encyclopédique du « *Centre for Agricultural Bioscience International* », en cours de développement, regroupe quant à elle déjà 1300 fiches au niveau mondial). Dans un contexte de changements globaux et de paysages agricoles changeants (voir Veres *et al.* 2011, Bianchi *et al.* 2006 pour la nécessité d'une approche régionale), le contrôle des insectes est devenu de plus en plus difficile (Pei *et al.* 2010), notamment pour les ravageurs envahissants. Pour anticiper sur les pics d'émergence des insectes et conduire des actions de lutte adaptées, le recours à la modélisation comme outil d'aide à la décision s'est aujourd'hui généralisé (*e.g.* modèles de pression parasitaire, Estay *et al.* 2009).

Fig. 9 : Dégâts de la teigne de la pomme de terre *Tecia solanivora* sur un tubercule dans les Andes équatoriennes.

3.2. Modélisations des insectes ravageurs des cultures

Depuis le développement du système PMEX[8] d'aide à la décision en 1975 (voir Welch 1984 pour une révision de la littérature sur les premiers développements de modèles informatiques d'aide à la décision en protection intégrée des cultures), de nombreuses approches de modélisation continuent de contribuer à la lutte contre les ravageurs des cultures. Dans les pays des zones tempérées, la surveillance journalière du climat avec la généralisation des stations météorologiques associées aux connaissances accrues sur la biologie des ravageurs ont permis des avancées considérables pour pouvoir anticiper sur les pics d'émergences des insectes, et protéger ainsi les cultures efficacement (*e.g.* Leskinen *et al.* 2011). Si la plupart de ces outils sont à l'échelle de l'exploitation, le passage à l'échelle du paysage, nécessite la prise en compte explicite de ce paysage (voir Veres *et al.* 2011). Pour représenter la dynamique dans le temps et dans l'espace de ravageurs des cultures, les modèles mécanistiques spatialement explicites constituent des outils tout indiqués (Lopes *et al.* 2010), en permettant de relier les comportements observés (*e.g.* dispersion, choix reproducteurs) à l'hétérogénéité spatiale du paysage (Vinatier *et al.* 2012), sous l'hypothèse d'une hétérogénéité explicative de la répartition des populations. Pour étudier cette hétérogénéité, il est important de se situer au niveau d'organisation adéquat, du gène à la communauté, en passant par l'individu ou la population (Witham *et al.* 2006). A titre d'exemple, le niveau d'organisation de l'individu permet de suivre l'évolution des caractéristiques propres de chacun d'entre eux, ce qui n'est pas nécessairement pertinent lorsque le paysage est représenté à une résolution faible (*e.g.* lorsque la dispersion est faible par rapport à la zone d'étude considérée, voir Vinatier *et al.* 2011), bien que le changement de niveau d'organisation puisse se faire au détriment de propriétés pouvant émerger des interactions entre individus (voir Grimm 1999 pour une révision de la littérature sur les modèles individu-centrés). Les modèles de type automate cellulaire ou individu-centrés sont donc utilisés en fonction du questionnement, du modèle d'étude, du contexte, de l'échelle et de la résolution considérée (*e.g.* Duehl *et al.* 2011 pour un automate cellulaire régional d'un ravageur des forêts ou Arrignon *et al.* 2007 pour un modèle individu-centré d'un auxiliaire des cultures). La figure 10 illustre des changements dans le niveau d'organisation dans la représentation des pucerons en fonction de l'échelle et de la résolution considérée.

[8] Pest Management EXecutive

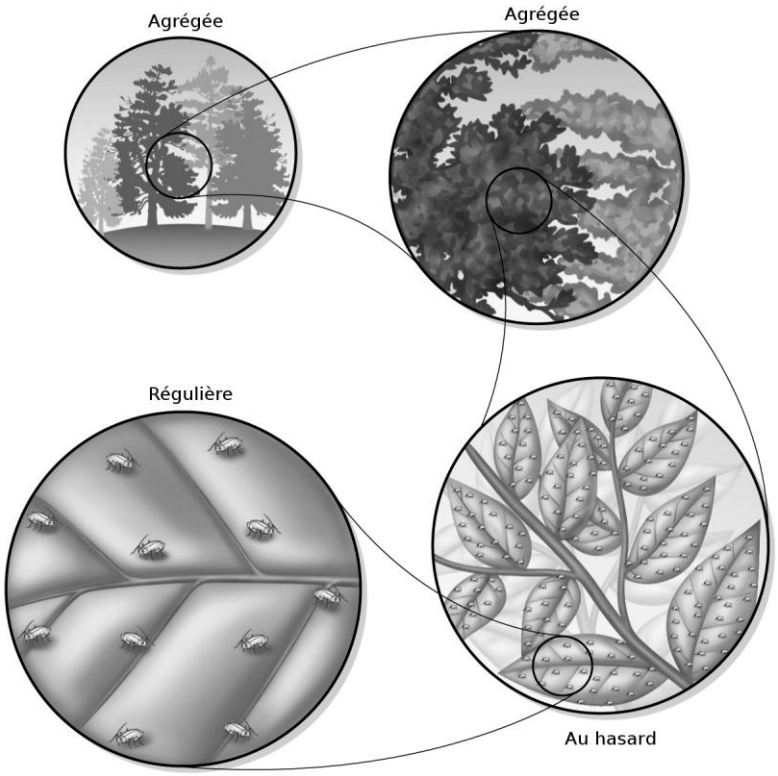

Fig. 10 : Répartition spatiale de pucerons en fonction de l'échelle d'observation. En fonction de cette échelle et de la résolution considérée, le niveau d'organisation dans la représentation des pucerons est différent (de la communauté aux individus) (d'après Townsend *et al.* 2008).

4. Contexte de travail

4.1. Enjeux, challenges et objectifs

Les systèmes socio-écologiques agricoles sont des systèmes complexes au sein desquels la dynamique spatio-temporelle d'insectes ravageurs des cultures constitue une propriété émergente du système (*i.e.* le produit des processus d'auto-organisation entre entités, voir Corning 2002). Si l'approche socio-écologique est de plus en plus présente dans les études d'usage des sols (Murray-Rust *et al.* 2011 ; Matthews *et al.* 2007), elle reste un challenge majeur pour les agrosystèmes tant au niveau social qu'écologique (Epanchin-Niell *et al.* 2010), alors même que l'avenir des populations humaines repose sur la maîtrise du pilotage des services écosystémiques assurés par les agrosystèmes (supposant la compréhension des mécanismes sous-jacents) (Galic *et al.* 2012). Bien qu'indispensables pour répondre à ces enjeux, le développement de modèles aux complexités adaptées aux questions pour lesquels ils seront construits soulèvent une série de défis (à toutes les étapes du cycle de développement), dont les plus significatifs seraient :

- au niveau conceptuel :
  - Quels niveaux d'organisation devraient être considérés (gènes, individus, populations, communautés, autres) ?
  - Quelles entités seraient à intégrer au système représenté (sociales et écologiques) et quels sont les interactions entre ces entités ?
  - Quelle connaissance avons-nous de chacune d'elles et à quel niveau d'abstraction pourrions-nous nous situer ?

- au niveau méthodologique :
  - Quels types de modèles pourraient être utilisés (AC, SMA, autres) ?
  - Comment utiliser ou coupler les modèles existants de chaque champ disciplinaire, puis comment valider de tels modèles ?
  - Comment capturer et analyser des propriétés émergentes (temporelles, spatiales, fonctionnelles) ?
  - Concernant les acteurs du système étudié, comment s'élaborent les décisions individuelles ? Comment formaliser et intégrer les perceptions des acteurs ?
  - Comment arriver à des solutions durables (*i.e.* comment mobiliser les acteurs et les rassembler autour d'une vision commune des systèmes socio-écologiques et de leur évolution) ?
  - Comment évaluer des stratégies en cours ou à venir ? Comment en communiquer les résultats ? Si l'objectif est la construction de scénarios prospectifs, quelles fiabilités pourraient y être associées ?

A travers l'exemple d'un complexe d'espèces de teignes de la pomme de terre (voir Rondon 2010 pour une révision de la littérature sur leur biologie, écologie et contrôle) dans le nord des Andes[9], et à divers niveaux d'abstraction, ce manuscrit propose d'apporter sa contribution à la réflexion sur la modélisation de la dynamique spatio-temporelle de ravageurs des cultures dans les systèmes socio-écologiques. De manière plus générale, l'objectif est de contribuer à une meilleure compréhension et intégration des activités humaines en modélisation de la biodiversité.

[9] Le lecteur trouvera une description des systèmes socio-écologiques du nord des Andes tropicales dans le chapitre 1 (Crespo-Pérez *et al.* 2011) et le chapitre 3 (Dangles *et al.* 2010).

4.2. Données sociales et écologiques

La qualité des données est déterminante pour le développement et la validation des modèles (Belovsky 1994). Pour répondre à ses objectifs, ce travail repose notamment sur des données écologiques de terrain collectées depuis 2006 dans les Andes équatoriennes, étendues par l'auteur depuis 2009 au Pérou et à la Bolivie (réseau de surveillance du complexe d'espèces de teignes de la pomme de terre au moyen de pièges à phéromones, voir le site Internet du projet http://www.innomip.ird.fr et Fig. 11 pour la cartographie des sites). A ces données de surveillance s'ajoutent les expérimentations de terrain et de laboratoire antérieurs, dont les résultats ont servi de base pour l'écologie des teignes (voir Dangles *et al.* 2008, Puillandre *et al.* 2008, Dangles *et al.* 2009, Hernandez *et al.* 2010, Torres *et al.* 2011). Les données sociales ont été obtenues majoritairement par des enquêtes auprès des agriculteurs rencontrés lors des campagnes de surveillance de l'abondance des teignes, et grâce au soutien de nombreuses institutions locales. Ces données écologiques et sociales ont été complétées par une révision de la littérature présentée au sein de chacun des chapitres de ce manuscrit.

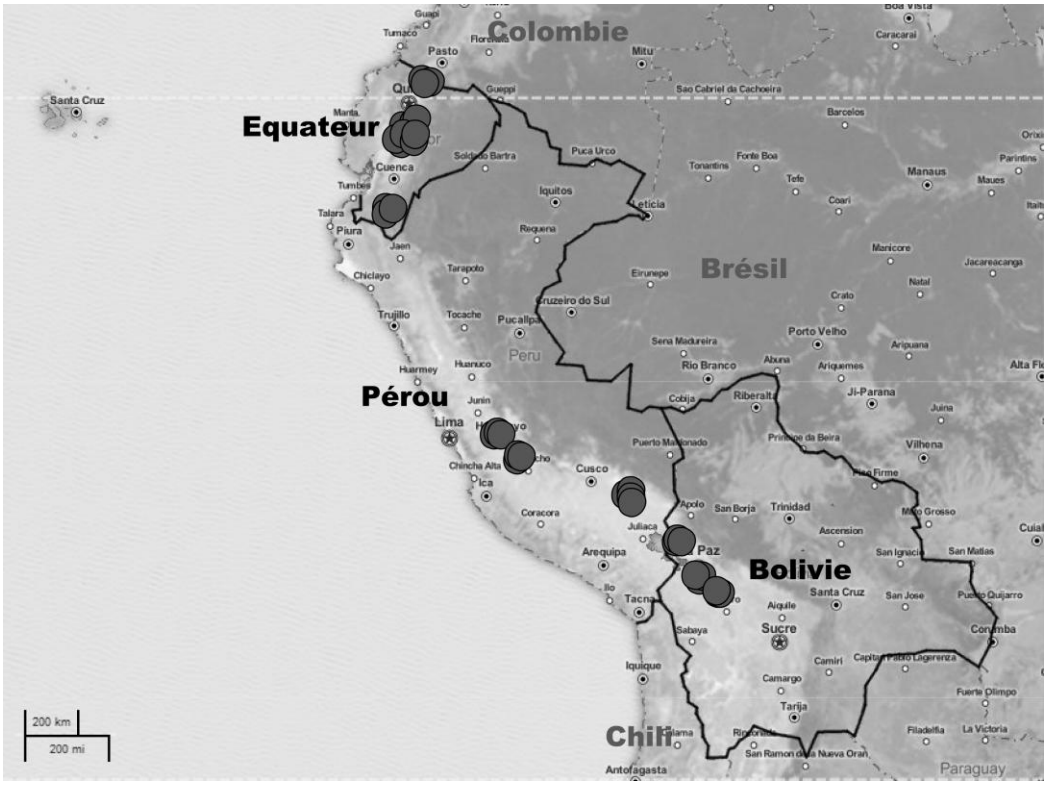

Fig. 11 : Cartographie des 6 zones de surveillance des abondances des espèces de teignes de la pomme de terre dans les Andes entre 2009 et 2012 (nord, centre et sud de l'Equateur, centre et sud du Pérou et nord de la Bolivie). Chaque site (55 au total), représenté par un rond gris, comporte un thermomètre et trois pièges à phéromones pour les trois espèces de teignes de la pomme de terre. Ils ont été relevé tous les 15 jours par des agriculteurs ou des techniciens, ces derniers centralisant l'information sur une base de donnée en ligne développée par l'auteur (voir http://www.innomip.ird.fr).

5. Organisation du manuscrit

Les résultats de ce manuscrit sont organisés en trois chapitres sur la base des objectifs et du contexte des modèles développés (voir Fig. 12 qui est reprise en début de chaque chapitre), à des niveaux d'abstraction variables au sein de chaque chapitre.

Chapitre 1 – En intégrant un paysage spatialement explicite, ce chapitre traite de l'hétérogénéité spatiale et de son influence sur la dynamique spatio-temporelle des insectes ravageurs. Il considère les niveaux d'organisation de l'individu à la population, à travers un modèle individu-centré et un automate cellulaire, respectivement. Les échelles considérées sont locales et régionales. Cette dernière échelle permettra l'identification de facteurs humains dans la dispersion des insectes sur le paysage agricole.

Chapitre 2 – Dans ce chapitre, l'accent est porté sur les activités humaines et à l'influence des stratégies de lutte sur la dynamique spatio-temporelles des insectes. Plus particulièrement, il se propose d'étudier et d'évaluer de manière théorique puis appliquée, comment une innovation agricole liée au contrôle des ravageurs se diffuse et quelles en sont les conséquences dans un système socio-écologique à l'échelle d'une communauté d'agriculteurs du nord des Andes. Il aborde la notion de couplage entre modèles de type automates cellulaires et agent-centrés, ou les agents représentent des groupes d'agriculteurs.

Chapitre 3 – Dans ce dernier chapitre, c'est la recherche participative et la communication des résultats qui sont abordées. L'objectif est de participer à une réflexion sur la formation à la protection intégrée des cultures dans les pays du Sud et de contribuer au développement d'outils interactifs innovants de formation pour assurer la durabilité des systèmes socio-écologiques.

Fig. 12 : Représentation schématique de l'organisation du manuscrit.

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CHAPITRE 1 - MODELISER LA DISPERSION D'ESPECES ENVAHISSANTES DANS UN PAYSAGE HETEROGENE

Chapitre 1 - Modéliser la dispersion d'espèces envahissantes dans un paysage hétérogène

Dans ce chapitre, l'auteur s'est intéressé à l'hétérogénéité du paysage dans lequel les insectes évoluent, et à la manière dont il était possible de représenter et d'intégrer cette hétérogénéité de manière explicite dans les modèles (paysage physique et social). Derrière cette réflexion, la question centrale était de savoir quelle était l'influence de l'hétérogénéité spatiale sur la dynamique spatio-temporelle des insectes, et donc de savoir si son intégration apportait une valeur ajoutée aux modèles existants.

Dans un premier temps, l'auteur a plus particulièrement étudié la teigne de la pomme de terre dans les Andes en collaboration avec Verónica Crespo-Pérez (aujourd'hui titulaire d'un doctorat réalisé sous la direction d'Olivier Dangles) *et al.*, qui a donné lieu à un article scientifique dans la revue *Landscape Ecology* et au sein duquel la participation en tant que co-auteur a été significative dans les phases de développement, d'analyse, de rédaction et de révision. Le modèle développé est de type automate cellulaire, le niveau d'organisation est la population d'insectes, l'échelle est régionale et la résolution de 500 mètres par 500 mètres.

Dans un second temps, en collaboration avec Arnaud Le Rouzic (chargé de recherche CNRS en génétique travaillant sur les relations entre phénotypes et génotypes au Laboratoire Evolution, Génome et Spéciation) *et al.*, l'auteur a cherché à intégrer les adaptations locales des insectes imputables à l'hétérogénéité d'un paysage modifié par l'homme. L'approche de modélisation était en conséquence insecte-centrée, chaque insecte étant porteur d'un bagage génétique spécifique. L'échelle et la résolution sont génériques dans cette approche à un fort degré d'abstraction.

Ce sont ces deux articles qui constituent le premier chapitre de ce manuscrit de thèse dont voici les citations :

Crespo-Pérez V., **Rebaudo F.**, Silvain J.F., Dangles O. (2011) Modeling invasive species spread in complex landscapes: the case of potato moth in Ecuador. ***Landscape Ecology*** 26, 1447-1461.

Rebaudo F., Le Rouzic A., Dupas S., Silvain J.F., Harry M., Dangles O. (***à soumettre***) SimAdapt: An individual-based population genetics simulation model in managed landscapes.

1.1. Modéliser la dispersion d'espèces envahissantes dans un paysage complexe : le cas de la teigne de la pomme de terre en Equateur

Résumé en français

Les zones tropicales d'altitude sont colonisées par l'homme depuis longtemps et bien que ces zones soient vulnérables aux invasions biologiques, elles n'ont reçu que peu d'attention au regard de la littérature existante. Cependant, la compréhension de la dynamique des ravageurs envahissants dans des paysages socio-écologiques agricoles, comme dans les Andes tropicales, est à la fois un défi et une nécessité pour les écologistes, compte tenu des retombées potentielles pour les pays en voie de développement qui affrontent les problèmes croissants causés par ces ravageurs. Dans cette étude, la réhabilitation d'une route reliant une vallée éloignée des Andes équatoriennes a constitué une zone d'étude privilégiée pour étudier la propagation spatiale d'une teigne de la pomme de terre envahissante au sein d'un paysage agricole non-infesté. Pour ce faire, il a été utilisé un modèle d'automate cellulaire pour représenter la dynamique spatio-temporelle de la teigne. L'intégration de variables empiriques a permis d'étudier l'influence relative de l'hétérogénéité du paysage au niveau environnemental et au niveau social sur la dispersion de la teigne. Deux types d'activités anthropiques ont été étudiées en particulier: (1) la présence et la distribution spatiale des structures traditionnelles de stockage de la pomme de terre qui modifient le microclimat local et (2) la dispersion à longue distance de teignes induite par les déplacements humains. Les données de surveillance participative des niveaux d'infestation du ravageur dans la zone d'étude et une enquête de terrain à l'échelle des Andes équatoriennes ont permis de valider le modèle sur la base des présences/absences relevées. Les simulations ont révélé qu'une densité forte et une distribution groupée des structures de stockage favorisait l'invasion des teignes (en modifiant la température du paysage), tout comme la dispersion passive à longue distance induite par l'homme. La confrontation du modèle aux données de terrain a permis d'affiner la précision et le réalisme des simulations en incluant les composantes sociales mentionnées du paysage. Ce travail se traduit par la mise à disposition d'une structure méthodologique puissante et adaptable soulignant l'importance cruciale d'intégrer le paysage social pour développer des modèles d'invasion précis de ravageurs des cultures dans des systèmes agricoles complexes.

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

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Abstract

Tropical mountains have a long history of human occupation, and although vulnerable to biological invasions, have received minimal attention in the literature. Understanding invasive pest dynamics in socio-ecological, agricultural landscapes, like the tropical Andes, is a challenging but timely issue for ecologists as it may provide developing countries with new tools to face increasing threats posed by these organisms. In this work, road rehabilitation into a remote valley of the Ecuadorian Andes constituted a natural experiment to study the spatial propagation of an invasive potato tuber moth into a previously non-infested agricultural landscape. We used a cellular automaton to model moth spatio-temporal dynamics. Integrating real-world variables in the model allowed us to examine the relative influence of environmental versus social landscape heterogeneity on moth propagation. We focused on two types of anthropogenic activities: (1) the presence and spatial distribution of traditional crop storage structures that modify local microclimate, and (2) long-distance dispersal (LDD) of moths by human-induced transportation. Data from participatory monitoring of pest invasion into the valley and from a larger-scale field survey on the Ecuadorian Andes allowed

us to validate our model against actual presence/absence records. Our simulations revealed that high density and a clumped distribution of storage structures had a positive effect on moth invasion by modifying the temperature of the landscape, and that passive, LDD enhanced moth invasion. Model validation showed that including human influence produced more precise and realistic simulations. We provide a powerful and widely applicable methodological framework that stresses the crucial importance of integrating the social landscape to develop accurate invasion models of pest dynamics in complex, agricultural systems.

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.

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

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).

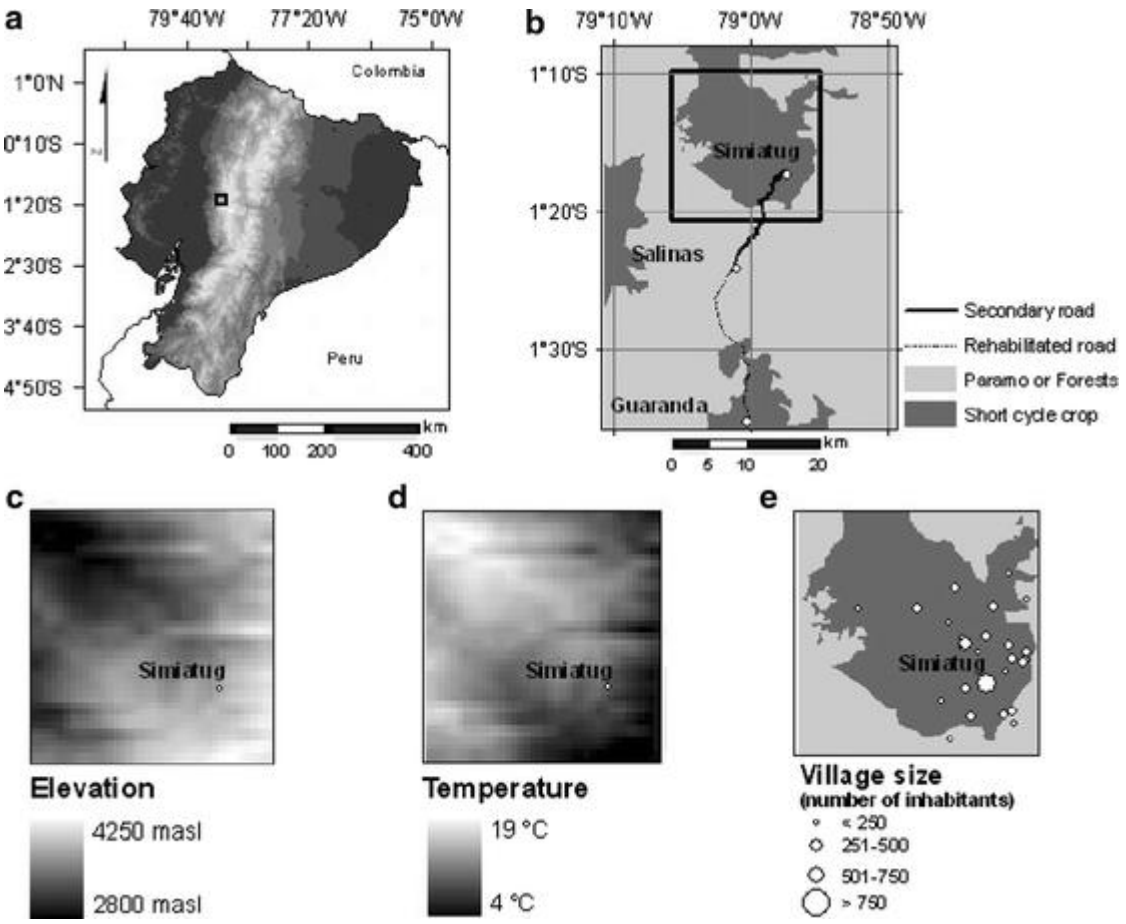

Fig. 1 Map of the study area showing a the location of the Simiatug Valley in the central Ecuadorian Andes; b land use in the area showing the specific area of 20 × 20 km of our cellular automaton (black square); c elevation of the cells of our grid; d mean yearly temperature of the last 30 years of 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)

Altitudes of the Simiatug valley range from 2,800 to 4,250 m (Fig. 1c). Its climatic conditions are typical of the Ecuadorian Andes where mean temperatures vary more with altitude than with season (Fig. 1d) (Dangles *et al.* 2008). Diurnal temperatures vary dramatically and the pattern of hot days and cold nights overshadows temperature variations through the year. Rainfall also shows little seasonality and varies on a local basis (see climate graphs in Dangles *et al.* 2008, Appendix A, http://www.esapubs.org/archive/appl/A018/062/appendix-A.htm). Such stable climatic conditions permit potatoes to be grown all year, and cause the agricultural landscape to be made up of a mosaic of potato fields at various stages of maturation. This, along with the presence of stored potato tubers in traditional shelters, means that food for moth larvae is always available. These conditions likely explain why neither diapause nor seasonal rhythms have been reported for this species

at any elevation in Ecuador and imply that its thermal limits and population dynamics are defined spatially rather than seasonally (Dangles *et al.* 2008). About 25,000 people, mainly subsistence and market-oriented farmers, currently live in the Simiatug parish in about 45 Kichwa communities or in scattered houses across the territory. With approximately 3,000 inhabitants, Simiatug village is the economic center of the valley and the communities around are smaller in size and density (50–700 inhabitants) (for further detail see Dangles *et al.* 2010).

The model

Overall structure

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

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→j) as follows:

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

where the first factor represents the probability of a vehicle carrying infested potatoes leaving an infested village, and the second one represents the attractiveness of a non-infested village (note that there were 26 villages in our study area).

The first factor is influenced by village size (human population relative to that of Simiatug village, W i = 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:

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

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).

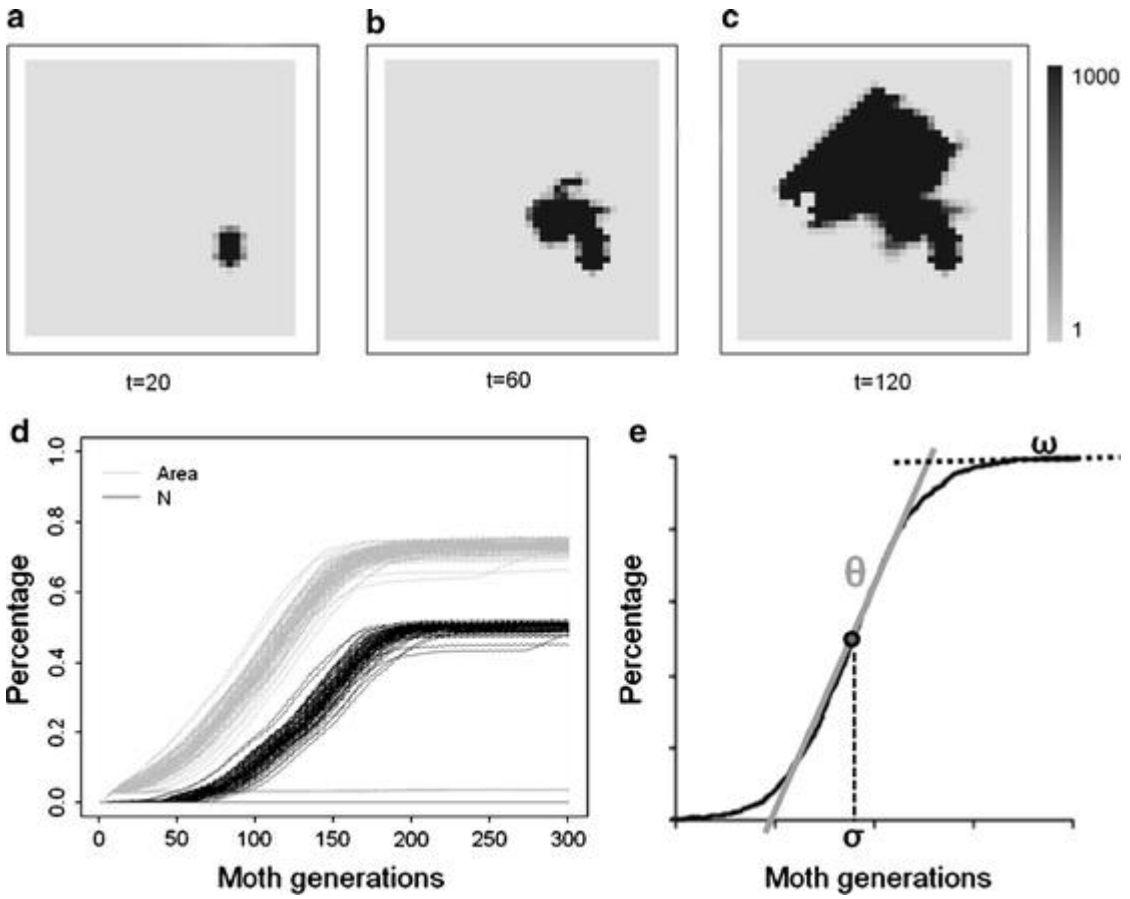

Fig. 2 Examples of model outputs: a–c spatial invasion represented by captions of CA grids at three different steps (t) of the invasion process; d temporal invasion throughout moth generations with the relative number of moths (N) and the proportion of invaded area (Area); e sigmoid wave showing the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

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).

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.

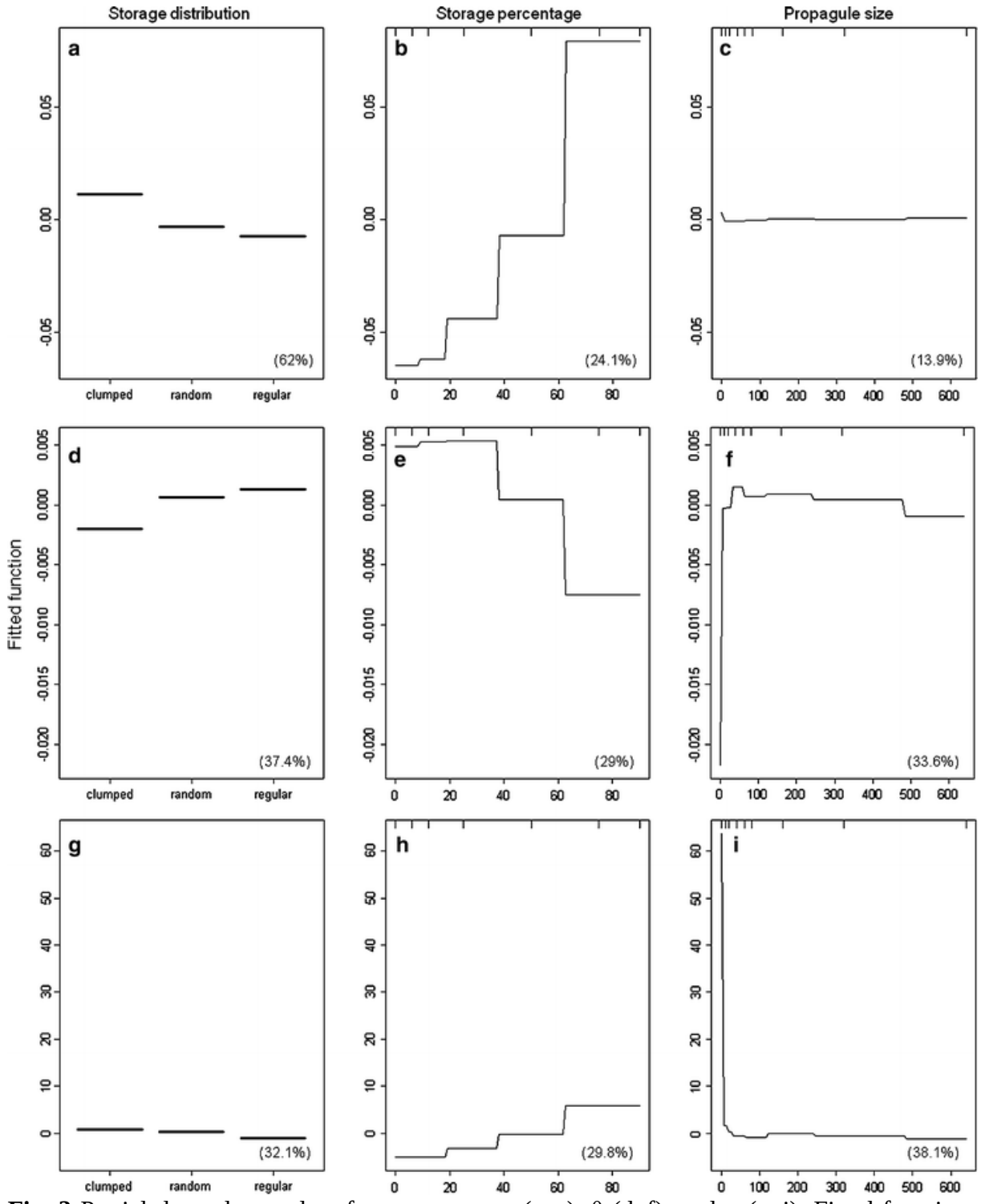

Fig. 3 Partial dependence plots for parameter ω (a–c), θ (d–f), and σ (g–i). Fitted functions have been centered by subtracting their mean. Rug plots at the inside top of plots show the distribution of data, in deciles, of the variable on the X-axis. Values in parenthesis indicate relative contribution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

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

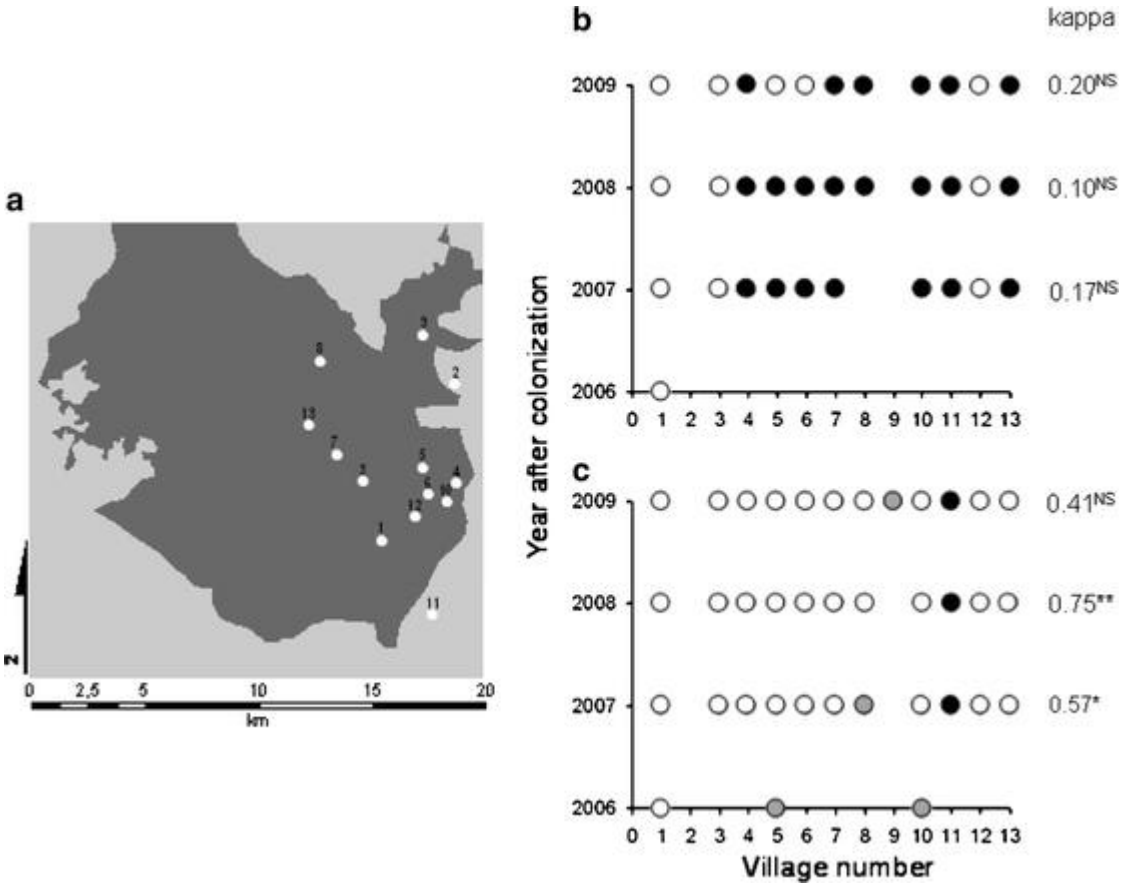

Fig. 4 Spatio-temporal validation of the model's outputs to field monitoring data from 2006 to 2009 in the Simiatug valley. a The 13 villages involved in the monitoring; b outputs of the basic model (no human influence); c outputs of the LDD scenario. Black circles represent cases where moths were observed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

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).

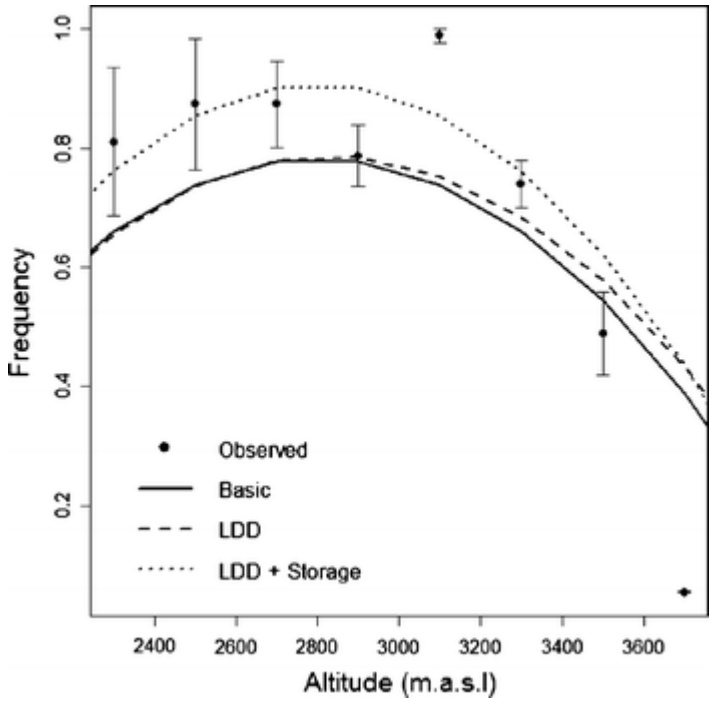

Fig. 5 Altitudinal validation of the model's outputs to field monitoring data in the Ecuadorian Andes. The figure shows the comparison between the observed altitudinal distribution in 85 sites of central Ecuador where moth abundance was sampled between 2006 and 2009 and predicted distribution by the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

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 (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.

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1.2. Un modèle de simulation individu-centré de génétique des populations dans des paysages modifiés par l'homme

Résumé en français

Les programmes informatiques sont devenus des outils essentiels pour l'analyse des données de génétique du paysage. Pour l'analyse de ces données, il existe divers logiciels génériques et efficaces, mais lorsqu'il s'agit de simuler des données sur un paysage modifié par l'homme, les modèles alors disponibles sont souvent trop spécifiques d'un type de question ou d'un modèle d'étude en particulier. Dans cet article est présenté un modèle de simulation individu-centré spatialement explicite de génétique du paysage, pour représenter les processus évolutionnaires d'adaptation et la dynamique des populations d'une espèce dans un paysage modifié par l'homme. Les sorties de ce modèle peuvent être directement analysées en utilisant les logiciels de génétique des populations les plus usuels, avec un module d'échantillonnage virtuel. Ce logiciel libre a été conçu pour être convivial, il fonctionne sur les systèmes d'exploitation les plus courants et est facilement adaptable à différentes questions ou situations biologiques. De l'exploration de scénarios au regard du potentiel d'adaptation d'une espèce à des changements environnementaux, jusqu'aux impacts de la gestion de l'usage des sols sur la structuration des populations, ce modèle de simulation peut être utilisé dans une large gamme de situations et représente un outil prometteur pour les scientifiques, les étudiants et les enseignants à la recherche d'une plateforme pratique et pédagogique pour explorer des situations empiriques ou théoriques.

SimAdapt: An individual-based population genetics simulation model in managed landscapes

Manuscript Draft

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Keywords: individual-based model; simulation; ecology; landscape; population genetics; spatially explicit

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Running title: Simulation model for landscape genetics

Abstract

Computer programs are essential tools in modern landscape genetic data analysis. The analysis of collected data is usually performed by various efficient computer software based on different frameworks, but simulation models to explore scenarios of a changing landscape are generally task or model specific. We developed a spatially explicit, individual-based, landscape genetic simulation model to represent evolutionary processes of adaptation and population dynamics in a changing landscape. The simulation output can be directly analyzed using popular population genetic programs, with a virtual sampling model. Our free software has been designed to be user-friendly, cross-platform and easily adaptable to different questions and biological situations. From the exploration of scenarios regarding species potential of adaptation to environmental changes, to the impact of land use management on species structure, this simulation model can be used in a broad range of contexts and represents a promising tool for scientists, students and professors looking for a practical and pedagogical framework to explore both empirical and theoretical situations.

Introduction

While population genetics is based on mathematical models of growing complexity, the spatial and temporal complexity of population dynamics and its interaction with a changing landscape remains often ignored (Epperson *et al.* 2010). However, in the context of global change, in order to understand the impact of evolutionary forces and local adaptive genetic variation in natural populations and individuals, it is necessary to integrate spatial and temporal variations of landscape (Manel and Segelbacher 2009). It is especially true when considering that natural populations do not meet the assumption of the simplest population genetics models, given the heterogeneity of landscape both in space and time resulting in a deviation from panmixia and/or Hardy-Weinberg equilibrium (Landguth *et al.* 2011). Documenting and predicting rapid evolutionary changes in response to natural or human caused environmental changes requires a deep knowledge of biological systems, including the genetic architecture of traits under selection and local landscape data. Landscape genetics seem to be well indicated to this challenge considering this scientific field combines the interaction between landscape and both neutral and adaptive genetic changes (Holderegger *et al.*, 2010). However, explicit landscape genetics require sophisticated simulation tools to explore the impact of natural selection, genetic drift, migrations, and mutations within heterogeneous landscapes (Balkenhol and Landguth 2011). In this context, individual-based models (IBMs) appear to be particularly adapted tools (Balkenhol and Landguth 2011;

Landguth *et al.* 2010a). Recent studies using IBM revealed that the power of this approach could be used for a broad range of model species, including fish to test the hypothesis of speciation with local adaptation (Gravilets and Vose 2005; Gavrilets *et al.* 2007), butterflies to identify patterns of speciation (Duenez-Guzman *et al.* 2009), birds to explore landscape change and its effects (Bruggeman *et al.* 2009; Bruggeman *et al.* 2010), or trees to explore the impact of exploitation on genetic diversity (Philips *et al.* 2004). In parallel, IBM approach has promoted significant improvement in generic software such as CDPOP (Landguth *et al.* 2010a; Landguth *et al.* 2010b; Landguth *et al.* 2010c), EcoGenetics (Jaquiéry *et al.* 2011), SimSSD (Legendre *et al.* 2002; Legendre *et al.* 2005), SPLATCHE (Currat *et al.* 2004) or KernelPop (Strand and Niehaus 2007) (see Hoban *et al.* 2012 for a review of computer simulations tools).

If scientists now dispose of reliable programs to analyze empirical data and connect population genetics to landscape, authors often have to spend considerable resources in developing their own simulation tools to explore and test empirical hypotheses *in silico*. Moreover, simulation models to explore scenarios of a changing landscape are generally task or model specific (Bonabeau, 2002). Simulation models are indeed often necessary to confront hypotheses with analyses and to explore the influence of given landscape configurations (Epperson *et al.* 2010). The addition of population dynamics to all other evolutionary forces (including selection in a multi-locus spatially-explicit changing landscape) is promising, but to our knowledge, a generalist simulation program of this type is still to be developed. Such a model should be generic enough to be applied to a broad range of species, and the corresponding software is expected to be user-friendly with a graphical user interface, cross-platform, easily available and easily extendable. While previous simulation approaches focus mainly on population genetics analysis, we have developed a generic simulation model that generates output directly usable into most-used and up-to-date population genetics computer programs (see Excoffier and Heckel 2006 for a selected list of computer programs). We describe the simulation model and proposed simple basic examples to illustrate its potential uses.

Methods

Simulation model

Our model simulates the evolution of a sexual, diploid population introduced in a landscape. It accounts for reproduction (with Mendelian inheritance), survival, dispersal (from immobility to panmixia) and adaptation to local conditions. This model combines an

individual-based, spatially explicit submodel (IBM) and a landscape cellular automaton submodel (CA) (see Fig. 1). Each time step in the model corresponds to one generation for individuals (generations are non-overlapping).

Cellular automaton: The CA, represented by a non-toroidal grid which dimensions are user-defined, includes a three-layer georeferenced information system to characterize the landscape: i) the available resources (carrying capacity for individuals, quantitative), ii) the landscape resistance (permeable or semi-permeable barriers for individuals, quantitative) and iii) the habitat type (natural selection for individuals, qualitative). These layers allow predicting separately the three major evolutionary forces (resource for population size and genetic drift, resistance for migration and habitat type for natural selection on loci under selection). The landscape characteristics can vary among space and time with different scenarios available for habitat types. These landscape management scenarios are: L1) no habitat type changes, L2) random changes, L3) changes to one of the nearest neighbor, and L4) emergence of new habitat types (or any user-defined scenarios). The variations among space are chosen in a list of landscape management scenarios (which can be easily extended in the code), and variations among time are user-defined.

Individual-based model: The IBM represents the individuals acting in the landscape (population dynamics and process of adaptation). Individuals are initially located either at a given set of coordinates or homogeneously over the landscape. They are characterized by a dispersal capability (maximum dispersal distance and rate of random dispersion among the possible locations allowed by the landscape resistance), and fitness trait for each habitat based on a set of loci under selection. The population genetics submodel within the IBM assumes one or several bi-allelic loci per habitat type. Possible alleles are either generalist (represented by "0"), or specialized (represented by "1") to the corresponding habitat type. Being specialized to a given habitat is considered advantageous while the individual is in the habitat, but deleterious in others habitats. This gene for habitat option was preferred to the allele for habitat option (one allele per habitat for each single locus), for its simplicity and realism. This allows the program to simulate efficiently multiple loci which is a key to analyze selection and speciation (Epperson *et al* 2012). Following the notation of Hartl (2005), the population genetics model considers a selection coefficient s against the deleterious genotype and a degree of dominance h of the deleterious allele. Consequently, at locus k specialized for habitat type i, j representing another habitat type, the selective values w of genotypes G_{11}, G_{10} and G_{00} (where the indices refer to the first and second allele at locus k under selection), are:

$$w_{G_{11,}k,i}=1 \quad \text{and} \quad w_{G_{11,}k,j}=1-s \qquad \text{Eq.1a}$$

$$w_{G_{10,}k,i}=1-sh \quad \text{and} \quad w_{G_{10,}k,j}=1-sh \qquad \text{Eq.1b}$$

$$w_{G_{00,}k,i}=1-s \quad \text{and} \quad w_{G_{00,}k,j}=1 \qquad \text{Eq.1c}$$

A multiplicative model with no epistasis is assumed, and the selective value of a given genotype is the product of the selective values at each locus (Wade *et al.* 2001):

$$W_{A,i}=\prod_{k=1}^{K} w_{G_A,k,i} \quad \text{with } A \text{ an individual on habitat type } i \qquad \text{Eq. 2}$$

For each given location (grid cell) in the landscape, individuals produce *f* offspring together, *f* being randomly chosen in a Poisson distribution (see Trajstman 1973):

$$f=min\left[C, X\sim Poisson\left(n\sum_{A=1}^{N} W_{A,i}/2\right)\right] \qquad \text{Eq. 3}$$

with *C* the carrying capacity of the grid cell, *n* the average number of offspring from a perfectly adapted individual ($W_{A,i}$ = 1), and N the number of adults present at the previous generation. For each of the *f* offspring, two parents are drawn randomly, proportionally to their fitness, and a gamete is generated from each parent. The genetic transmission follows the Mendelian inheritance laws, assuming free recombination between loci.

Neutral markers: In addition to the set of loci involved in adaptation, μ neutral independent loci (typically: microsatellite) can be considered. *Z* alleles can be present simultaneously in the population at each locus (at initialization, alleles are chosen in a normal distribution with a user-defined standard deviation conditioning the number of alleles and the expected heterozigosity, see Text S1 Fig. S3). Mutational events (rate *m*) replaces allele *z* by allele *z* +1 or by allele *z* -1, according to a classical stepwise mutation model. Neutral loci are transmitted according to the same rules as the loci under selection.

Model output: The characteristics of each individual are stored in a file including habitat type and coordinates (see Text S1 table S2 for an exhaustive list of characteristics). In order to allow direct comparison between simulated data and experimental data through popular software, the program includes an empirical destructive sampling module. A number of recollection points per habitat type is defined by the user, each of them with a given number of sampled individuals (see Zurell *et al.* 2010 for a discussion on sampling in simulation models and Schwartz and McKelvey 2009 in landscape genetics). The program

then creates a file containing the microsatellite genotype of all sampled individuals in a format that can be processed by most-used population genetics software (Excoffier and Heckel 2006) including GENEPOP v4.1 (Rousset 2008), ARLEQUIN v3.1 and v3.5 (Excoffier *et al.* 2005), STRUCURE v2.3.3 (Pritchard *et al.* 2000; Falush *et al.* 2003; Falush *et al.* 2007; Hubisz *et al.* 2009) and GENELAND v3.3 (Guillot *et al.* 2005a; Guillot *et al.* 2005b; Guillot *et al.* 2008; Guillot 2008; Guillot and Santos 2009; Guillot and Santos 2010) (see Table 1 for a complete list of population genetics programs).

Implementation: A complete description and documented verification of the simulation model following the ODD protocol (Overview, Design concepts, Details) for describing individual- and agent-based models (Grimm *et al.* 2006, 2010) and the code using NetLogo multi-agent programmable modeling environment (Wilensky 1999) are provided as supplementary material (Text S1 and S2). The code is documented and structured in order to be modified and extended by non-modelers.

Study example

The example performed simulates the invasion of a diploid population of 100 individuals with μ=10 microsatellites loci introduced in the central cell of a landscape composed of two different habitat types (see Fig. 2a), on a homogeneous landscape (carrying capacity of 100 individuals and resistance of 10% per cell) over a squared territory of 5 per 20 grid cells. Individuals can disperse up to one cell with a rate of dispersion of 0.5. The average fitness of the reference genotype is ten offspring with a coefficient of selection of s = 0.5 against other genotypes and a dominance degree of h = 0.5. Mutation rate was fixed to 10^{-4} per locus per generation. Regarding the distribution of alleles at neutral loci, introduced population was initialized with a standard deviation of 1, corresponding to less than 10 different alleles and around 70% of heterozygosity (see Text S1 and Fig S3), for each independent locus. Simulations were repeated five times during 100 generations and output sampled with 20 random recollection points per habitat type with 25 individuals per recollection point every five generations. Three different habitat type configurations were tested: C1) random location of habitat types with landscape management scenario L2 (see Fig. 2a), C2) blocs of habitat types with scenario L1 (*i.e.* no changes, see Fig. 2b) and C3) isolated habitat types with scenario L1 (see Fig. 2c). The simulation model provided comma-separated values files containing genotypes of all individuals at loci under selection and neutral loci (microsatellites), together with localization and generated input files for ARLEQUIN and GENELAND, containing sampled genotypes for neutral loci and localization in the

landscape. These files were created every 25 generations (*i.e.* four sets of files). Using ARLEQUIN (microsatellites), we generated basic output for both simulations with the expected and observed heterozygosity and fixation index F_{ST} (considering the individuals in each habitat type as separated populations). We then used GENELAND (microsatellites) to visualize the correlation between habitat types and population differentiation using coordinates of sample points, assuming that up to 5 different populations could exist (see Fig. 3a, b, and c). In Figure 4 (a, b, and c), using comma separated values files, we mapped the distribution of allelic frequencies at a locus under selection using all individuals.

Results of the simulation example

Results after 100 generations are presented in Table 2. For the three landscape configurations, the observed and expected heterozygosity were similar within an habitat type, while the fixation index F_{ST} between individuals located in the two habitat types was greater for landscape configuration C2. Regarding population assignment, the five populations identified by GENELAND were separated by a geographical horizontal gradient in the case of the landscape configuration C2 (Fig. 3b), and to a lesser degree in the case of C2 (Fig. 3a), while in the case C3 (Fig 3c), populations obtained were intermediate between an horizontal gradient and the habitat type pattern. In this last case, the mapping failed to give a clear delimitation of populations in some simulations, induced by the randomness of the sampling and the high migration rate. The mapping of the allele frequencies situated on a locus under selection (mapping of allele "1" of the locus corresponding to habitat type 1, see Fig. 4abc) revealed an homogeneous repartition in the case of landscape configuration C1 (Fig. 4a), while in configuration C2 and C3, where habitat types were grouped and fixed over time, we observed high frequencies close to one in habitat type "H1" and low frequencies close to zero in habitat type "H2" (see Fig. 4b and 4c, respectively). Intermediate zones between habitat types showed average frequencies (gray scale). The availability of neutral loci (population assignment and mapping on the basis of microsatellites) and loci under selection (allele frequencies at a locus under selection) provided complementary information that is generally not accessible using empirical data (loci under selection unknown). This exemplifies the relation between habitat discontinuity, clines in genes under selection and neutral markers clusters.

Discussion

Our study case reproduced the pattern classically observed when modeling the dynamics of species invasion starting with the introduction of few individuals in a landscape (see Hamilton 2009). These classical situations re-evaluated through a more complex spatial and temporal dynamics provide an example of the possibilities offered by our simulation model (see also Balkenhol and Landguth 2011), leading to a better understanding of the spatial pattern of genetic variation (see Sork and Waits 2010 for contributions expected from landscape genetics).

Of course, when implementing the model, we made a series of choices and assumptions, and yet, the documented code provided as supplementary material should allow any scientist with basic skills in programming to modify it to his convenience. For example, the population genetics submodel of adaptation, although general, which might not be well-suited to every study model (*e.g.* more than two alleles at adaptation loci, epistatic interactions, etc), could be easily modified to fit a particular case. So does the ecological submodel, which remains rather simple considering individual behavior (random dispersal and mating). Indeed, the dispersal rate of individuals is non-density dependent and dispersion occurs randomly, when some species can have a perception of habitat quality over neighboring habitats and consequently behave differently (see salamanders example by Devitt *et al.* 2011). Thanks to intensive collaboration between disciplines, this model was structured to represent an ideal tool for interdisciplinary communication and has the potential to be extended to address these issues, between others, in a near future (see Balkenhol *et al.* 2009 for future research needs in landscape genetics). However, the need to store the genotype of each individual with fluctuating population sizes and density on a changing landscape limits the landscape size or resolution that can be considered in the model, as already identified by Landguth *et al.* 2010b. Due to obvious computational limits, very large grids cannot be processed efficiently. Nevertheless, we managed to simulate 100 generations using the example parameterization in a 100 per 100 grid cells with up to one million individuals in approximately 5 hours using a recent computer, which should be sufficient to address most cases in practice. Beside this limitation, from a deep thinking about resolution should emerge the identification of the appropriate spatial and temporal scales, one of the identified challenges in landscape genetics (Balkenhol *et al.* 2009).

This simulation model demonstrated the ability to represent traditional patterns documented in the literature (see Hartl 2005, Hamilton 2009). Moreover, thanks to its modularity, this software represents a unique tool to explore the interactions between gene

flow, population dynamics, selection, and landscape management. With its changing landscape feature, it should contribute to the required development of more sophisticated alternative hypotheses to the null hypothesis of isolation by distance (Segelbacher *et al.* 2010). Relying on an individual-based model, this framework allows the integration of real world patterns including spatially explicit landscape changing over time (see also Landguth *et al.* 2011). Along with existent software on population genetics analysis, it allows direct comparison with empirical data. Moreover, this simulation model that produces genetic data from population dynamic scenarios could easily be used in a backward approach within Approximate Bayesian Computation framework to infer population dynamics parameters from genetic data (Hoban *et al.* 2012). From empirical studies to theoretical cases, it should facilitate our understanding of landscape genetics and represents a promising tool for both scientists and students willing to explore heterogeneous complexity.

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Figure legends

Fig. 1. Representation of the model. It comprises an individual-based submodel (individual) coupled with a cellular automaton submodel (landscape). Management refers to the way landscape change over time for the tree layers (available resources, landscape resistance and habitat type). Adaptation as described here is an emergent property of the simulation model and occurs between generations.

Fig. 2. Landscape configurations for the example with (a) random location of habitat types with landscape management scenario L2, (b) blocs of habitat types with scenario L1 (*i.e.* no changes) and (c) isolated habitat types with scenario L1, respectively referred as landscape configurations C1, C2 and C3.

Fig. 3. Frequencies of the allele "1" at the locus under selection of the first habitat type (a, b, c) corresponding to landscape configurations C1, C2 and C3, respectively. The allele frequencies in (a, b, c), range from one, in white, to zero, in black. Only one simulation is represented per landscape configuration after 100 generations.

Fig. 4. Results of the population assignment using GENELAND (a, b, c) corresponding to landscape configurations C1, C2 and C3, respectively Each color represents a different population and each "plus" a point sampled. Only one simulation is represented per landscape configuration after 100 generations.

Tables and figures

Figures

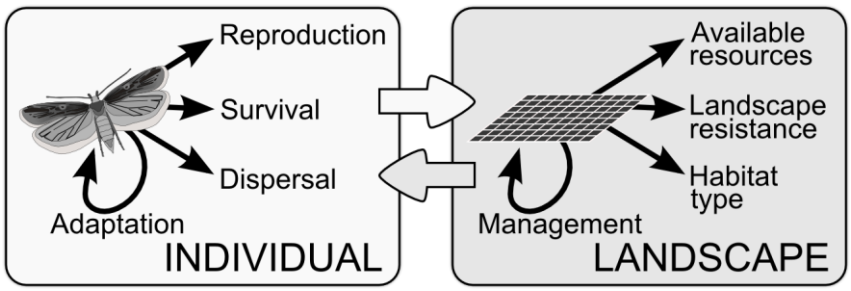

Fig. 1 *(two-third page)*

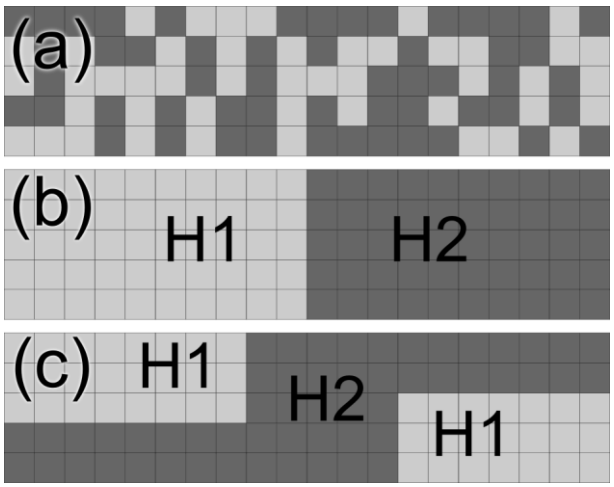

Fig. 2 *(one column)*

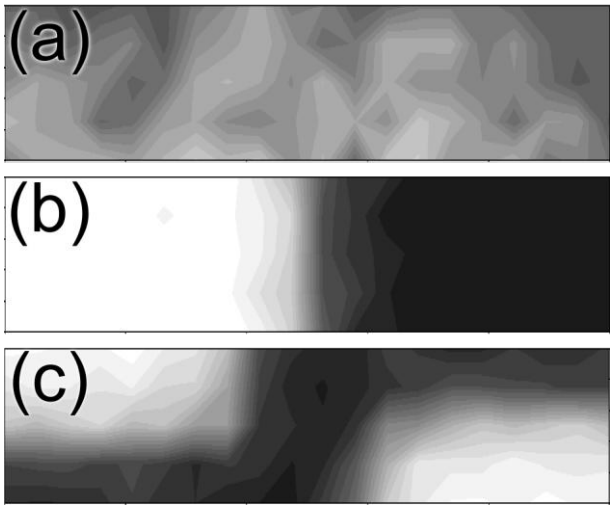

Fig. 3 *(one column)*

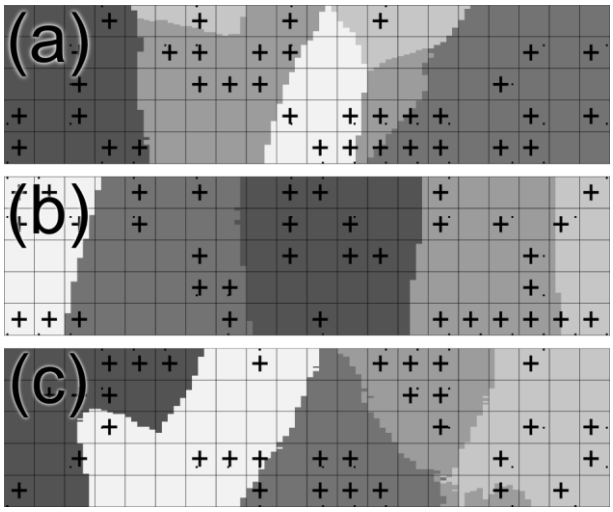

Fig. 4 *(one column)*

Tables

Table 1. Computer programs input files for population genetics data analysis generated by the simulation model

Name	Version	References
ARLEQUIN	3.1 and 3.5	Excoffier *et al.* 2005
GENEPOP	4.1	Rousset 2008
FSTAT	2.9.3	Goudet 1995
STRUCTURE	2.3.3	Pritchard *et al.* 2000; Falush *et al.* 2003; Falush *et al.* 2007; Hubisz *et al.* 2009
GENELAND	3.3	Guillot *et al.* 2005a; Guillot *et al.* 2005b; Guillot *et al.* 2008; Guillot 2008; Guillot and Santos 2009; Guillot and Santos 2010

Table 2. Output of the model after 100 generations analyzed using ARLEQUIN v3.5 with 95% confidence intervals. Each simulation has been repeated five times.

Landscape configuration	C1		C2		C3	
Habitat type	H1	H2	H1	H2	H1	H2
Observed heterozygosity	0.68 [0.67;0.69]	0.69 [0.68;0.70]	0.67 [0.66;0.68]	0.69 [0.68;0.71]	0.69 [0.67;0.70]	0.68 [0.66;0.70]
Expected heterozygosity	0.70 [0.70;0.71]	0.70 [0.69;0.71]	0.69 [0.68;0.69]	0.70 [0.69;0.71]	0.70 [0.69;0.71]	0.70 [0.69;0.71]
Fixation index F_{ST}	0.0016 [0.0008;0.0025]		0.0363 [0.0327;0.0400]		0.0033 [0.0025;0.0041]	

Supplementary material

Text S1. Extended presentation of the model following the ODD protocol together with validation and verification documentation.

Text S2. Model code using NetLogo (Wilensky 1999).

CHAPITRE 2 -

APPROCHES PLURIDISCIPLINAIRES ET COUPLAGE DE MODELE SOCIAL ET ECOLOGIQUE

Chapitre 2 - Approches pluridisciplinaires et couplage de modèle social et écologique

Le chapitre précédent a abordé l'hétérogénéité spatiale du paysage en démontrant son importance pour la dynamique spatio-temporelle d'espèces envahissantes. Il a intégré des aspects pluridisciplinaires sous forme de modules (*e.g.* dispersion à longue distance, structures de stockage, génétique des populations), sans pour autant réellement coupler des modèles issus de disciplines différentes. Ce chapitre traite du couplage entre un modèle social de diffusion de l'information et un modèle écologique précédemment décrit d'écologie des populations. Dans ce modèle social, l'auteur a cherché à intégrer le comportement d'agriculteurs et plus particulièrement la prise de décision au sein d'une communauté hétérogène d'agriculteurs. L'objectif, à travers ce couplage, est d'apporter une contribution à l'intégration explicite des activités humaines dans la compréhension de la dynamique spatio-temporelle d'insectes ravageurs des cultures.

Dans un premier temps, l'approche est théorique et tente, au-delà de l'aspect novateur de la démarche, d'identifier des pistes pour parvenir à évaluer des campagnes de sensibilisation à la protection intégrée des cultures. Elle a donné lieu à un article scientifique dont une deuxième version révisée à été soumise le 4 avril 2012 à la revue *Environmental Modelling and Software* à l'occasion d'un numéro spécial sur la modélisation multi-agents pour les systèmes socio-écologiques.

Dans un second temps, nous avons étudié à nouveau le cas de la teigne de la pomme de terre dans les Andes, compte tenu de la quantité et qualité des données récoltées depuis 2006 par l'équipe IRD-PUCE en Equateur, sans qui cette étude n'aurait pu aboutir. Ce travail a donné lieu à un article publié dans la revue *PLoS Computational Biology*.

Ce sont ces deux articles qui constituent le deuxième chapitre de ce manuscrit de thèse dont voici les citations :

Rebaudo F., Dangles O. (***en révision***) An agent-based modeling framework for integrated pest management dissemination program. ***Environmental Modelling and Software.***

Rebaudo F., Dangles O. (2011) Coupled Information Diffusion - Pest Dynamics Models Predict Delayed Benefits of Farmer Cooperation in Pest Management Programs. ***PLoS Computational Biology*** 7:10.

2.1. La modélisation multi-agents : un outil pour définir des stratégies de lutte contre les ravageurs dans des communautés hétérogènes d'agriculteurs

Résumé en français

L'acquisition et de la diffusion de l'information au sein d'une population hétérogène de personnes a beaucoup été étudié en sciences sociales. Cependant, peu d'approches ont été développées pour mieux comprendre comment les patrons et les processus de diffusion de l'information affectent la gestion de ressources dans des systèmes socio-écologiques complexes. C'est cependant une question opportune pour les programmes de protection des plantes qui sont plus que jamais à l'ordre du jour des politiques internationales en raison du nombre croissant de défis liés au contrôle des ravageurs des cultures. Pour évaluer l'impact de comportements hétérogènes d'agriculteurs et les types de diffusion de l'information (actif ou passif) sur le succès d'une campagne de protection intégrée des cultures (IPM), nous avons développé un modèle socio-écologique couplant un modèle de ravageur des cultures (croissance et dispersion) avec un modèle comportemental des agriculteurs (contrôle des ravageurs et diffusion des pratiques de gestion). L'objectif principal du modèle était d'explorer des stratégies de diffusion de l'information dans un contexte de protection intégrée des cultures. Nos simulations ont révélé que 1) la diffusion IPM passive de l'information parmi les agriculteurs semblerait être plus efficace pour contrôler le ravageur à l'échelle du groupe d'agriculteurs que la diffusion active et que 2) les niveaux croissants d'hétérogénéité dans le comportement des agriculteurs ralentiraient significativement la dynamique de contrôle du ravageur, mais dans une moindre mesure dans le cas de la diffusion passive de l'information. Nos découvertes suggèrent donc que des programmes de diffusion IPM doivent concentrer leurs efforts dans le développement de méthodes générant des conditions propices à l'apprentissage, tout en intégrant les limitations dues à l'hétérogénéité des comportements des agriculteurs. Notre étude démontre de plus l'importance du développement d'une plateforme permettant de faire le lien entre données sociales et écologiques, dans le temps et dans l'espace, dans un contexte de gestion des systèmes agricoles. Bien que dans cette étude, nous nous soyons concentrés spécifiquement sur des niveaux d'infestation de ravageurs et des stratégies de diffusion IPM de l'information, notre approche pour comprendre la diffusion de l'information au sein de populations humaines hétérogènes en interaction avec des variables

environnementales serait applicable dans un contexte plus large, intégratif des aspects sociaux et des questions de gestion de ressources.

An agent-based modeling framework for integrated pest management dissemination program

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Abstract

The study of how people acquire and diffuse information among heterogeneous populations has a rich history in the social sciences. However, few approaches have been developed to better understand how information diffusion patterns and processes affect resource management in complex socio-ecological systems. This is a timely issue for crop protection diffusion programs, which have a larger place than ever on the international policy agenda due to the growing number of challenges related to controlling agricultural pests. To assess the impact of heterogeneous farmer behaviors (receptivity toward IPM practices) and types of information diffusion (either active or passive) on the success of integrated pest management (IPM) programs, we developed a socio-ecological model coupling a pest model (population growth and dispersion) with a farmer behavioral model (pest control and diffusion of pest management practices). The main objective of the model was to provide insights to explore effective IPM information diffusion strategies at the farmer community level. Our simulations revealed 1) that passive IPM information diffusion among agents seemed to be more effective to control pest over the community of agents than active diffusion and 2) that increasing levels of agent heterogeneity would significantly slow down pest control dynamics at the community level, but to a lower extent in the case of passive IPM information diffusion. Our findings therefore suggest that IPM diffusion programs should focus their efforts in developing methods to create purposefully the conditions for social learning as a deliberate pest control mechanism, while taking into account potential limitations related to the commonly reported farmer heterogeneity. Our study further stresses the need to develop a

comprehensive and empirically based framework for linking the social and ecological disciplines across space and time in agricultural system management. While we specifically focus on pest infestation levels and IPM information diffusion strategies in this study, our approach to understand information diffusion within heterogeneous human populations in interaction with environmental features would be applicable to a much wider range of both social and resource management issues.

Software availability

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Year first available: 2012

Software required: NetLogo 5.0 (Wilensky 1999)

Program language: NetLogo

The model description using the Overview, Design concepts and Details protocol (Grimm *et al.*, 2010) can be found in Appendix A and the model itself in Appendix E (alternatively it can be obtained by contacting the authors). The model requires the Open Source multi-agent programmable modeling environment NetLogo which can be downloaded at http://ccl.northwestern.edu/netlogo/.

1. Introduction

Pest invasions can adversely affect agricultural practices and natural resources, imposing significant economic and environmental costs (Pimentel *et al.*, 2005). While the probability of pest spread mostly depends on the pest management options in place (Hashemi *et al.*, 2009; Peshin and Dhawan, 2008), most spread models treat in detail the spatial aspects of the spread but lack the capability to incorporate the effect of control actions on further spread of the species (Cacho *et al.*, 2010). Consequently, pest control strategies worldwide are mostly based on the ecological characteristics of pest species or environment (Vuilleumier *et al.*, 2011), and rarely consider the social environment in which pests spread (Khuroo *et al.*, 2011; Larson *et al.*, 2011). In the specific case of agricultural systems, the social environment is critical to understand pest spread as control actions mostly lie in the hand of farmers (either individuals or organized groups), whose behaviors have been shown to depend on a wide array of social (*e.g.* network structure) and ecological factors (*e.g.* pest dispersion) (Epanchin-Niell *et al.*, 2010).

Worldwide, the lack of pest management competences is one of the main reasons why farmers fail to control pest attacks (Hashemi *et al.*, 2009; Nyeko *et al.*, 2002). This is

especially true in the case of emergent invasive pests for which farmers have no pre-existing local knowledge and consequently have different perceptions and attitudes (García-Llorente *et al.*, 2008). Over the past decades, extension science has developed several approaches towards farmers to promote pest control information diffusion (Van den Berg and Jiggins, 2007), including modeling techniques (Voinov and Bousquet, 2010). Information diffusion processes, based on theories of information dissemination (Brenner 2006), can fit into two main categories, passive and active (Röling and Wagemakers 1998). On the one hand, passive diffusion relies on the spread of pest control information and behaviors arising from innate mimicry among farmers (*e.g.* Collins, 2004). Fowler and Christakis (2010) have shown that behaviors can indeed cascade in human social networks even when people interact with strangers or when reciprocity is not possible; people mimic the behavior they observe and this mimicking can cause behaviors to spread from person to person to person (*e.g.*, social learning sensu Bandura 1977). On the other hand, active information diffusion relies on a spread of pest control information and behaviors arising from a limited number of farmers who train other farmers about pest control practices. This approach has been adopted by most participative integrated pest management (IPM) programs (*e.g.*, farmer field schools, Van den Berg and Jiggins, 2007; Feder *et al.*, 2004) and relies on the assumption that farmers may benefit training other farmers as it would prevent invasive pests present in the field of neighbors to re-infest their own fields. Both types of information diffusion have been classically observed in a wide array of agricultural situations (Schreinemachers and Berger, 2011; Feder *et al.*, 2006; Rogers, 2003; Berger, 2001).

Because behaviors and perceptions towards new information and technology can vary widely among farmers belonging to the same community (Dangles *et al.* 2010, Berger 2001), farmers' behavioral heterogeneity is a key issue to understand and predict the success of pest control information diffusion throughout the community, and therefore the success of the IPM program at a large scale (Paredes 2010). Moreover, farmers' decisions about whether to diffuse (or not) pest control practices from/to other farmers will be closely dependent on pest infestation in their own field (Peshin and Dhawan, 2008). This means that IPM information diffusion will be tightly linked to pest dynamics at the community level, itself depending on pest ecology and control behaviors of all farmers. The specification of IPM strategies in terms of the proportion of active vs. passive IPM information diffusion therefore requires the coupling of ecological and sociological models, an approach which has, to our knowledge, never been applied to IPM issues (Rebaudo and Dangles, 2011). In this context, agent-based models (ABM) may represent ideal tools to provide new theoretical insights into the

sustainable development of farmers' control practices (Berger 2001; Bousquet and Le Page 2004; Liu *et al.*, 2010; Smajgl *et al.*, 2011). Although ABM have increasingly been applied to physical, biological, medical, social, and economic problems (Bagni *et al.*, 2002; Bonabeau 2002; Grimm *et al.*, 2005; Freeman *et al.*, 2009; Parott *et al.*, 2011) it has been, to our knowledge, disregarded by IPM theory and practice. The model developed here explored, via numerical simulations, the consequences of IPM strategies on pest population dynamics, under several assumptions regarding farmer behavioral heterogeneity (theoretical receptivity toward innovation) and farmer decision-making (short term benefits).

To explore theses strategies, we developed an ABM coupling a pest model to a behavioral model of farmer decisions. The pest model estimates pest population levels over time, while the behavioral model estimates IPM information diffusion from farmer to farmers. The behavioral model includes a social network range, which determines the possible interactions an agent can have with other agents and represents the environment in which information diffusion can occur (Choi *et al.* 2010, Kuandykov and Sokolov, 2010, Oreszczyn *et al.*, 2010). Consequently, it would likely influence how IPM information would diffuse in the agricultural landscape. The pest model includes the pest dispersal rate, which determines indirectly the influence that one farmer pest control actions have on neighborhood farmers. If a farmer perceives the pest as a secondary threat (defined as a pest whose population rarely reaches intolerable levels), and if the pest has high dispersion capabilities, then its lack of control would enhance infestation into the field of other farmers even if they apply control practices (Epanchin-Niell *et al.*, 2010). In this complex system, pest infestation levels at the community scale emerge from the collective actions of IPM information diffusion and pest control among agents.

The general design of our ABM was determined from pest-landscape interactions, pest-farmer interactions, and inter-farmer interactions. In our model, pest control information diffuses among agents with heterogeneous behavior, and aggregate performance is measured as the mean pest infestation level over the community.

2. Material and methods

2.1. Model overview

Our socio-ecological model comprises three key elements: the agricultural landscape, the pest population, and the farmers (Fig.1). The agricultural landscape represents a community of farmers composed of n farms, themselves divided into z fields. The whole community is therefore represented as a grid of n x z elementary cells (600 farmer's fields

with n = 100 farms or agents) in which the pest disperses and becomes established following a cellular automaton process (see Rebaudo *et al.* 2011 and Crespo-Perez *et al.* 2011 for similar approaches). Pest dynamics was simulated through a logistic growth function (Verhulst, 1977), with pest dispersion occurring from one field to the Von Neumann neighborhood fields (see details in Appendix A). In each time step (equivalent to one pest generation) the infestation grew and spread over farms territories. To build our ABM we populated the agricultural landscape with n artificial agents, each of them representing a group of people working in the same farm (farm households as decision-making units, see Solano *et al.*, 2006). In our model, agents attempted to control pest densities and we assumed that their success in doing so was dependent on the IPM information they possess. A full description of the model is provided in Appendix A using the Overview, Design concepts, Details (ODD) protocol (Grimm *et al.* 2006, 2010).

In this study, we simulated a situation in which agents had no pre-existing knowledge to control the pest (as in the case of an emergent invasive pest), *i.e.* their initial level of IPM information k = 0 (with k ranging from 0 to 5, based on IPM information distribution characterized in a previous study, see Rebaudo and Dangles 2011). We then assumed that y agents were trained to control the pest (simulating farmers trained through an extension program) and therefore set up the level of pest control of these agents to 5. We then carried out ABM simulations to assess the importance of two key social factors on the success of the IPM program at the community level: 1) the way the information acquired by trained agents diffused throughout the community and 2) the heterogeneity in individual agents' receptivity towards IPM practices.

2.2. IPM information diffusion

We compared two types of IPM information diffusion: 1) A passive diffusion in which agents mimic behaviors they observed from other agents having higher IPM information (and therefore better control practices), and causing behaviors to spread from agent to agent to agent. 2) An active diffusion (training) where agents with higher IPM information trained other agents about effective pest control practices (thereby increasing their IPM information) (see Fig.1).

2.2.1. Agents' decision-making

In our model, agents choose among two alternatives: 1) they dedicate all their time to control the pest or 2) they share their time in equal proportion between pest control and IPM information sharing with other agents. To perform this decision, we made agents able to

perceive short-term benefits of their action (Stevens *et al.* 2005). Technically, agents minimize a function *Nt*, which represents the perceived pest infestation level *N* at a given time *t*. In our case we chose *t* = 1 (*i.e.* one time step) to simulate short term benefits. We assumed that:

$$N_1 = (1-c)N_0 + i - e \qquad \text{Eq. 1}$$

with *c* the pest control coefficient in a farmer's field, N_0 the current pest infestation level, *i* the proportion of the pest immigrating to a farmer's field from neighboring fields, and *e* the proportion of pest emigrating from farmer's field to neighboring fields (see more details in Appendix A). In the first alternative (full time dedicated to control the pest), an agent will perceive $i > e$ (they will receive high number of pests from their neighbors) while in the second alternative (time dedicated both to pest control and IPM information sharing), they will assume that $i = e$.

2.2.2. Passive diffusion

To simulate a passive diffusion process of IPM information throughout the farmer community we followed published ABM approaches developed to predict the spread of infectious diseases (*e.g.* Eubank *et al.*, 2004, Yu el al., 2010). We assumed that agents are more likely to learn when their own fields are infested by pests. Our experience (*e.g.* Dangles *et al.* 2010) showed that farmers having pest problems on their own farm are inclined to obtain information on pest control practices. In our model, an agent *a* could gain one unit of IPM information from any agent *b* with higher IPM information level and located within its social network (see Appendix A).

2.2.3. Active diffusion

Unlike passive diffusion where the initiative of gaining additional IPM information comes from an agent in need of more IPM information, active diffusion relies on a precept derived from the Farmer Field School (FFS) methodology (Van den Berg and Jiggins, 2007), in which farmers are encouraged to teach other farmers what they learn during the FFS (Feder *et al.*, 2004; Tripp *et al.*, 2005). In this case, the willingness to cooperate would be motivated, among other factors (*e.g.* financial incentives or interest in local self reliance), by the particular assumption that if neighbors of trained farmers do not adopt IPM measures, then the pests from their fields can re-infest the trained farmers' fields even if they apply IPM principles (Thomas, 1999). We assumed that agents are more likely to be taught when their neighbors' plots are infested as a consequence of the high pest levels in their own plots. In our

model, an agent *a* could train an agent *b* if this latter had a lower IPM information level and was located within its social network (see Appendix A).

2.3. Agent heterogeneity in IPM information acquisition

Farmers' attitudes towards IPM information acquisition are generally highly heterogeneous within a community (see Introduction). To integrate such heterogeneity into our model each agent was characterized by a "receptivity factor" *r* towards IPM practices (see Deroïan, 2002). This factor simulated agent's readiness to learn about new pest control practices and was assumed to be constant in the simulations (see Jeyaraj *et al.*, 2006; Feder and Umali, 1993). In our model *r* was fixed at initialization and distributed assuming a normal distribution of mean *mu* = 0.5 and a standard deviation *sd* ranging from 0 to 0.75. By modifying *sd* values in our simulations, we were therefore able to test for the effect of agents' heterogeneity on IPM information diffusion.

In addition, farmers' decision to learn about new pest control practices is generally tightly related to the level of pest *pi* in their own fields (see introduction). So we assumed in our model that the probability *P(learning)* of an agent *a* to learn additional IPM information ($k = k + 1$) during a information diffusion event with an agent *b* could be expressed as follows:

In the case of passive diffusion (see Eq.2):

$$P(learning) = pi_a * r_a \qquad \text{Eq. 2}$$

where pi_a is the pest infestation level in the farm of agent *a* and r_a the IPM receptivity factor of agent *a* (both ranging from 0 to 1).

In the case of an active diffusion (see Eq.3):

$$P(learning) = pi_b * r_a \qquad \text{Eq. 3}$$

where pi_b is the pest infestation level in the farm of agent *b* and r_a the IPM receptivity of agent *a* (both ranging from 0 to 1).

2.4. Model verification

The process by which an innovation or information gets adopted is traditionally modeled using the Bass model (Bass, 1969). One interpretation of the Bass model was that the time *t* from information training until adoption is assumed to have a probability distribution N_t, which can be expressed as follows (see Eq. 4):

$$N_t = N_{t-1} + p\left(m - N_{t-1}\right) + q\frac{N_{t-1}}{m}\left(m - N_{t-1}\right) \qquad \text{Eq. 4}$$

where p represents the coefficient of external influence, q the coefficient of internal influence and m the number of ultimate adopters.

This model has been widely used in marketing and management science (Sood *et al.*, 2009; Chance *et al.*, 2008). As the Bass model fits the data of almost all product introductions, we used it to verify our agent-based diffusion of information, thereby ensuring that our ABM correctly reproduces observed patterns in the literature (see Grimm *et al.*, 2005). In our case, we consider IPM information in its broader sense and can therefore take on various forms (*e.g.* IPM knowledge, products, practices). We therefore assumed that the functional form of the Bass model would reasonably represent the information sharing in our study system. Bass curve fitting to our ABM output data were performed following Kuandykov and Sokolov, 2010; and Cowpertwait and Metcalfe, 2009 (see Appendix B).

2.5. Model simulations

2.5.1. General model output

As presented above, the general design of our ABM was determined from pest-landscape interactions (*e.g.* dispersion from one field to another), pest-farmer interactions (pest control depending on agents' IPM information), and inter-farmer interactions (diffusion of IPM information among agents). We arbitrarily set up our ABM grid with n = 100 farms (and thereby 100 agents), z = 6 fields per farms, and y = 1 trained agent. While we are aware that any change in these parameters may affect model outputs, testing their importance was not the purpose of the present study. Instead, our focus was to investigate the impact of 1) the type of IPM information diffusion (active *vs.* passive) and 2) agent's heterogeneity (sd = 0, 0.25, 0.5 and 0.75) on the pest infestation level over the community. In addition we were interested in assessing how two other parameters, the range of agents' social network, and pest dispersion capabilities could influence our model outcomes.

2.5.2. Influence of farmer social network

To investigate IPM information diffusion we assumed, as proposed by Montanari and Saberi (2010), that social networks were dominated by geographic proximity. In our model, the social network of an agent corresponded to all agents situated in a geographical radius of s fields. Our simulation assessed the influence of social network radius on pest infestation levels with s values of 1, 3, 5, 7, and 9. Each s value was tested for both types of diffusion and the four levels of agents' heterogeneity.

2.5.3. Influence of pest dispersion

We performed a sensitivity analysis to assess the response of our model to variations in pest dispersion rates *d* with values of 0, 0.25, 0.5, 0.75, and 1. Due to the configuration of our landscape, no long distance dispersal events nor density dependent dispersion were integrated in the sensitivity analysis (see Carrasco *et al.*, 2010). Each *d* value was tested for both types of diffusion and the four levels of agents' heterogeneity.

2.5.4. Improving information diffusion strategies

As explained above, there was a fundamental difference between the two types of information diffusion we studied. On the one hand, passive diffusion was triggered by pest infestation levels in the fields of agents with low IPM information (*i.e.* these agents copy agents with higher IPM knowledge in order to increase pest control in their fields). On the other hand, active diffusion was initiated by agents with high IPM information. Both types of information diffusion have been used in IPM extension programs (Peshin and Dhawan 2008) and, because of the different diffusion processes involved, may be expected to work in a complementary way. To test this hypothesis, we used our model to explore whether we could find optimal proportions of active vs. passive diffusion events among farmers which would minimize pest infestation levels at the community level. To achieve this goal we performed a sensitivity analysis on the proportion (ranging from 0 to 1) of agents with active or passive IPM information diffusion and also tested how agents' heterogeneity would affect these results. We also tested the effects of pest dispersal rates and social network ranges on the outcomes of our model (see Appendix C).

3. Results

3.1. Model verification

For both active (Fig. 2A) and passive diffusions of IPM information (Fig. 2B), our results showed that the patterns predicted by our ABM were consistent with the Bass model ($P < 0.001$, see detailed statistics in Appendix B). The ability of our ABM to reproduce Bass model predictions therefore provided a verification of the correctness of information diffusion patterns among agents. Note that the Bass model has a poor fit in the early periods for both diffusion types as it assumes many early adopters of the innovation (while we had only one trained agent in our model).

3.2. Model simulations

3.2.1. Type of information diffusion and agent heterogeneity

Overall we found that the dynamics of pest infestation in the community was influenced by the type of IPM information diffusion throughout agents (Fig. 3). Passive diffusion generally allowed a lower pest infestation level to be reached more rapidly than active diffusion. Agents' heterogeneity had a significant impact on pest infestation levels at the community level with higher levels of heterogeneity producing (for both types of diffusion) higher pest infestation levels (Fig. 3). This positive effect of agents' heterogeneity on pest infestation levels was non-linear (S-shaped curve), as revealed by the pest infestation values observed at time = 50 generations. We also found that the effect of agent's heterogeneity on pest infestation levels was greater for active than for passive diffusion. Under our assumptions, average pest infestation levels are lower for teaching than for taught agents (the later having less IPM information). This implies that the probability of increasing IPM information level is higher through a passive than an active diffusion strategy. As a consequence, agents' heterogeneity has a greater impact on average pest infestation levels in a community of farmers involved in an active diffusion strategy.

3.2.2. Social network

The relationship between social network radius and pest infestation levels was not linear (due to the ratio between social network area and social network radius), with few differences in pest infestation levels when the network was ≥ 5 cells, and significant when the network was ≤ 3 cells (Fig 4A-H). Neither the type of IPM information diffusion nor the degree of agents' heterogeneity interacted with social network range to produce different patterns than those observed in Fig 3.

3.2.3. Pest dispersion capabilities

As stated in section 2.2.1., pest immigration and emigration (driven by pest dispersion rate) triggered agents' decision-making to diffuse IPM information (actively or passively). Consequently, the effect of pest dispersion rate on pest infestation levels was similar between the two types of IPM information diffusion (Fig. 4I-P). When agents exchanged IPM information through passive diffusion, higher rates of pest dispersion corresponded to lower pest infestation levels (Fig. 4I-L), although differences were small when compared to intermediate levels. As expected, in the case of active IPM information diffusion, we observed the same trend, with higher pest dispersion rates leading to lower pest infestation levels at the community scale (Fig. 4M-P) and high pest infestation levels with limited

dispersal rates (higher pest dispersion rates trigger more IPM information diffusion). For both types of diffusion, the influence of pest dispersal rates on pest infestation levels was greater at higher agents' heterogeneity.

3.3. IPM information diffusion strategies

Figure 5 shows the combined effects on overall pest infestation levels of agents' heterogeneity and the proportion between the two types of IPM information diffusion within the community of agents. This figure was obtained using fixed values of social network radius (s = 3) and insect dispersal rates (d = 0.5) (the way s and d influence pest infestation levels as a function of the proportion between the two types of IPM information diffusion was not different from conclusions drawn from Fig. 5, see Appendix C). Figure 5 confirmed that agents' heterogeneity led to higher pest infestation levels in the community, irrespective of the proportion between active and passive IPM information diffusion. Pest infestation levels were about 30-60% higher in communities with higher heterogeneity among agents. However, contrary to our expectations, we found that lower pest infestation levels were obtained when either only passive or only active IPM information diffusion was preferred. Unexpectedly, the highest pest infestation levels were systematically found for diffusion strategies mixing, at nearly equal levels of both types of diffusion.

4. Discussion

From the diffusion of innovations to rumors, financial panics and riots, and contagion-like dynamics, the study of the way people acquire information and the dynamics of how this information spreads among heterogeneous populations interacting through face-to-face communication has a rich history in the social sciences (Gächter and Herrmann 2009, Morone and Taylor 2004, Roger, 2003, Bass, 1969). However, few approaches have been developed to better understand how information diffusion patterns and processes affect resource management in complex socio-ecological systems. This is a timely issue for IPM diffusion programs as they have a larger place than ever on the international policy agenda due to the growing number of challenges related to controlling agricultural pests (Dangles *et al.*, 2009). In this context, our study sheds light on some of the factors and mechanisms that may affect pest control strategies based on the diffusion of IPM information throughout farmer communities.

4.1. Model limitations

Obviously, our agent-based modeling approach is a simplification of real-world systems and several limitations and improvements should be considered to better define its socio-ecological relevance. First our model assumes a strict overlap of spatial and social networks, which is a good approximation of reality for many isolated village communities in developing countries (Dangles *et al.* 2010). However, the increasing availability of communication technologies (*e.g.* cell phones) and mobility of farmers (Meera et al 2004) may result in a better connection of farmers to information than assumed in the model. Second, the rate of diffusion may be largely dependent upon the type of information considered such as its relative advantage for farmers, its compatibility within the social setting, its observability and simplicity (Fowler and Christakis 2010), which was not explicitly taking into account in our model. Also, personal networks in agricultural systems - where trusted people (prestigious individuals, people of authority or holding otherwise vested power and influence) often play a key role in decision making - are difficult to integrate into models due to their dynamic, multi-directional, and non-symmetric nature (Ferreira 1997). Third, we assumed a distribution of farmers' receptivity without any spatial structuring. While we acknowledge that zones of IPM-interested farmers may develop around patches of high pest populations, additional simulations of clustered farmer's receptivity revealed no effect on model outputs (results not shown but available in the code provided in Appendix E). Fourth, we assumed that less informed farmers applied lower pest control measures than well informed farmers. This may not be always the case, in particular in developing countries, where less informed farmers may apply high amounts of pesticides whereas better informed farmers would tolerate certain non-critical levels of pest infestation (Shetty 2004). Finally, while farmers usually tend to make high contributions in information diffusion initially, these tend to dwindle to low levels over time (Brush, 2004). Moreover, when information diffuses from person to person to person, the natural trend is an erosion of the initial information (Srithi *et al.*, 2009). We performed an additional sensitivity analysis integrating an "attenuation factor" in our ABM model, which reduced the effectiveness of IPM information diffusion depending on the number of nodes (*i.e.* distance in the social network) between the IPM information source (agent trained by external extension agents) and another agent (see Appendix D). This analysis revealed that, for both passive (Fig.D1 A-D) and active diffusion (Fig.D1 E-H), information erosion along the diffusion process would indeed delay the control of pest infestation, but not impede it.

4.2. Key factors affecting of IPM information diffusion

A first key factor affecting the dynamics of IPM information diffusion over our theoretical rural community was the heterogeneity of farmers in terms of IPM practices receptivity. Our results indeed revealed that increasing levels of agent heterogeneity would speed up pest infestation levels at the community scale (up to 60%) irrespective of the type of diffusion process (either passive or active). This corroborates a previous study on information diffusion among farmers by Foster and Rosenzweig (1995), which showed that information was expected to flow less smoothly in a heterogeneous population, particularly when the performance of new practices is sensitive to imperfectly transmitted information. Our findings are also in agreement with epidemiological models which generally show that heterogeneous populations enhance the spread of infections as well as make them harder to eradicate (for a review see Anderson 1992).

A second predictor of IPM program success seems to be related to the dynamics of the pest faced by farmers. One of the novelties of our approach was to merge a spatially explicit pest population dynamic model with a field-based multi-agent system describing farmer features and behaviors (see Milner-Gulland 2011 and Bousquet *et al.* 2001 for similar approaches in fishery and resource management, respectively). This implied that part of agents' decisions in the ABM relied on pest infestation levels in agents' fields, thereby mimicking real-world processes driving farmer decision to apply (or not) pest control strategies (see Peshin and Dhawan, 2008; Perez and Dragicevic, 2010). In the case of sedentary pest (defined as pests with low dispersal capabilities), neither active nor passive IPM information diffusion happened (Fig. C1 in Appendix C when insect dispersal rate is bellow 0.4). This suggests that IPM information diffusion may occur beyond a certain rate of pest dispersal, a feature previously reported in the agricultural extension literature (*e.g.* Witt 2008). However, additional studies would be needed to test for the validity of our findings with pests that disperse over long distances (see Crespo-Perez *et al.* 2011). In these cases, coordinated effort among farmers would be more promising than individual learning and teaching among neighbors.

Finally, a third key factor concerns the type of IPM information diffusion. In our simulations, passive diffusion was always more efficient than active diffusion to spread information among agents. This result can be explained by the fact that an agent will have a higher probability of increasing his IPM information through passive diffusion than in the active diffusion scenario (as "passive agents" generally have a higher pest infestation level than "active agents", due to their pest control information). While active information transfer

depends on both agents involved in the process of information sharing, passive information transfer mostly depends on the agent having a pest problem and looking for information to fix it. Also we assumed that farmers' receptivity followed the same distribution function in both diffusion types. Empirical data on farmers' behaviors and heterogeneity regarding IPM information diffusion would be needed to validate our model outputs and improve the socio-ecological relevance and generality of our modeling approach. Moreover, pest infestation levels through passive IPM information diffusion appear to be less negatively affected by farmer heterogeneity than for active diffusion. These results support the general assumption that social learning (sensu the process in which individuals observe the behavior of others and its consequences, and modify their own behavior accordingly, Bandura 1977) is often most efficient when communication between agents (*e.g.* social network range) is fairly limited (Morone and Taylor 2004, Ellison and Fudenberg 1995), and because spatial proximity such as found among farm neighbors is essential in the learning process of IPM information (Palis *et al.* 2005). IPM diffusion programs should therefore focus their efforts in developing methods to create purposefully the conditions for social learning as a deliberate pest control mechanism (see Ison and Watson 2007 for a broader discussion on the role of social learning in resource management issues). This could be achieved through technical improvements of IPM practices that would make them more attractive to farmers (see Affholder *et al.* 2010) such as the release of new products for pest control (*e.g.* a new bio-pesticide). Innovation often attracts farmers and could enhance social learning (see Peshin and Dhawan 2008). However, designing farmer field school sessions in which farmers would be taught about the potential effects of their individual vs. collective actions may be a relevant approach to speed up the diffusion of IPM information (*e.g.* Souchère *et al.*, 2010; Anselme *et al.*, 2010).

Unexpectedly, our theoretical simulations suggest that mixed strategies consisting of both passive and active diffusion processes should be avoided as they may slow down the dynamics of IPM information diffusion (see Fig. 5). Although validation with empirical data is needed, it is possible that, instead of being complementary, the combination of the two types of diffusion would jam IPM information diffusion. This result was partly attributable to the assumption that agents either diffused information passively or actively (but not both), which can create barriers to information diffusion. Simulations outputs differ in the case of agents shifting from one strategy to another (resulting in intermediate pest infestation levels between only passive or only active diffusion strategies see Fig. C3 in Appendix C). More information on farmers' profiles for information diffusion would be needed to improve our simulation results. Moreover, no multiplicative effects were identified as both strategies are

equally time consuming, which constrain the numbers of IPM information diffusion events during a time step.

4.3. Concluding remarks

Despite these limits the ability of our model to capture real-world patterns of information diffusion (Fig 2) indicates that our findings may yield important insights for IPM science and policies. One remaining challenge would be to perform empirical studies to calibrate our model with real world data. For example, the spatial structure of the agricultural landscape (*e.g.*, size, location, number of fields) could be defined from GIS layers from particular farmer communities (see Crespo-Pérez *et al.* 2011). Also the distribution of IPM information and its sharing efficiency among agents could be derived from field surveys (see Rebaudo and Dangles, 2011). To specifically test for effects on pest infestation levels of passive vs. active diffusion strategies, it would be possible to conduct empirical surveys following the release of an IPM innovation (*e.g.* a new bio-pesticide on the market) promoted through FFS. Inquests could be designed to identify whether farmers bought and applied the product after they were told by a trained farmer or if they approach the trained farmer themselves, attracted by the efficiency of the product.

In conclusion, our study stresses the need to develop a comprehensive and empirically-based framework for linking the social and ecological disciplines across space and time (see Liu *et al.* 2010). In our model, predictions of the coupled dynamic of pests and farmer behavior showed the evidence that farmer to farmer IPM information diffusion can help the broader community control pest infestation. Understanding the outcomes of heterogeneous IPM practices in farmer populations is a timely issue as IPM programs worldwide are confronting the reality of increasingly subdivided habitats managed as smaller areas. This reduces the likelihood that pest populations will be controlled at the individual level and thereby requires higher levels of information diffusion among farmers (Epanchin-Niell *et al.* 2010). In view of the growing importance of communication and cooperation issues for ecosystem management (see Rustagi *et al.* 2010 and references therein) we believe that our modeling approach may represent a valuable contribution to the increasing literature on resource management – society interactions.

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Figure list

Fig.1. Model schematization. A cellular automaton (modeling pest population dynamics in interaction with the agricultural landscape) is coupled to an agent-based model (farmer agents controlling pest and exchanging IPM information). Active and passive diffusion are explored with different levels of heterogeneity (receptivity toward IPM practices) among agents.

Fig.2. Simulated IPM information diffusion events over time fitted to the Bass model (black curve) for passive (A), and active IPM information diffusion (B). Each cross represents the mean of 100 simulations.

Fig.3. Pest infestation levels as a function of time at different levels of heterogeneity (receptivity toward IPM practices) with passive diffusion (A) and active diffusion of the IPM information (B). Each curve is the mean of 100 simulations during 100 time steps.

Fig.4. Sensitivity analysis on 1) the social network variable for passive (A-D) and active diffusion of IPM information (E-H) and 2) the pest dispersal rate variable for passive (I-L) and active diffusion of IPM information (M-P). Pest infestation levels are represented over time for 5 values of social network ranges and 5 values of dispersal rate for different levels of heterogeneity (receptivity toward IPM practices sd = 0; 0.25; 0.5; 0.75). Each curve is the mean of 100 simulations during 100 time steps.

Fig.5. Effect of combined agents' heterogeneity and proportion of IPM information diffusion type (active vs. passive) on mean pest infestation level in the community at time t = 100 steps. On the Y scale, a proportion of 0.2 means 20% of passive and 80% of active IPM information diffusion. A total of 121 couples of values (receptivity toward IPM practices *i.e.* agents' heterogeneity; proportion of IPM diffusion type) were simulated 100 times and were averaged to obtain mean pest infestation levels in the community (represented by a grey gradient ranging from 0 to 1). Confidence Intervals (CI95%), are represented in the right side of the figure using the same grey gradient and scale.

Figures

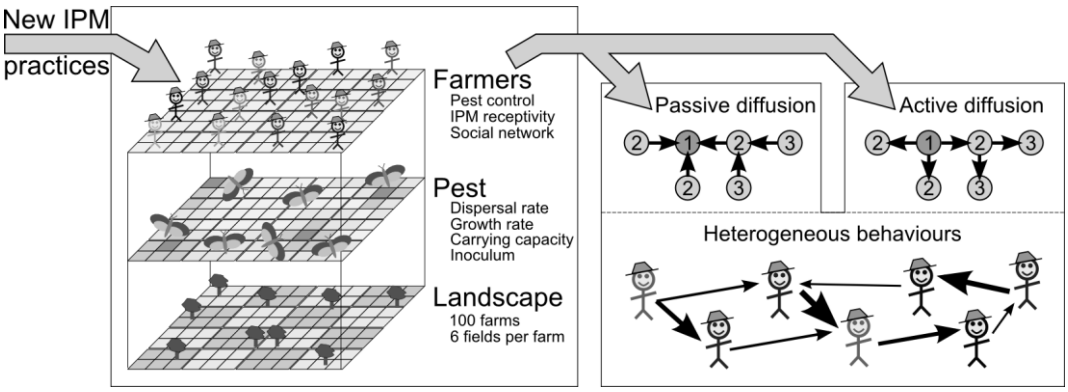


Fig. 1

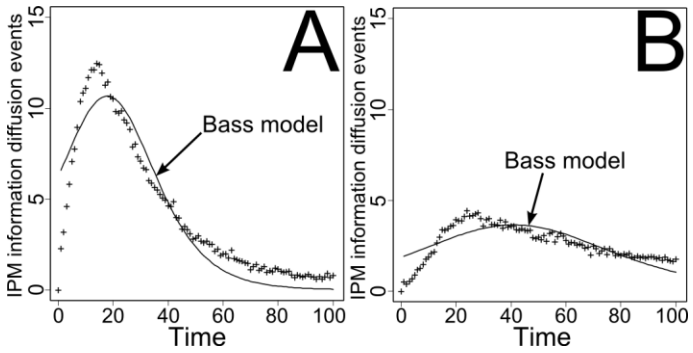


Fig. 2

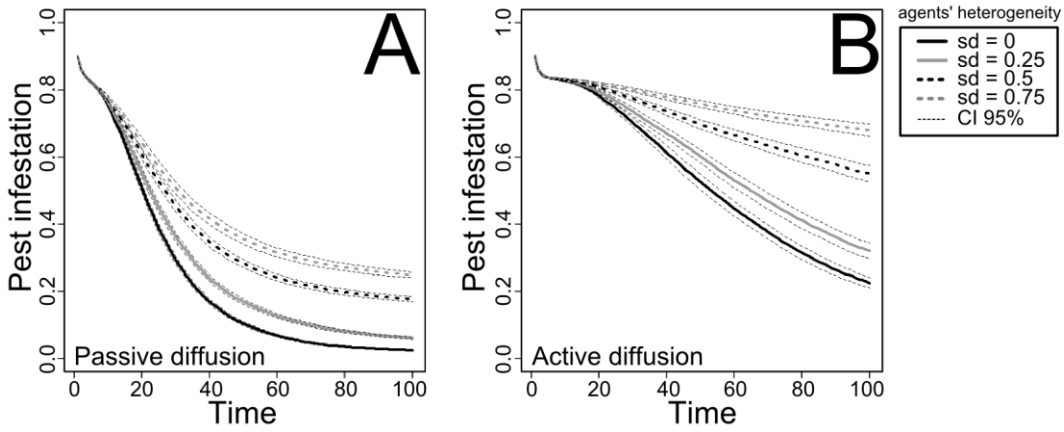
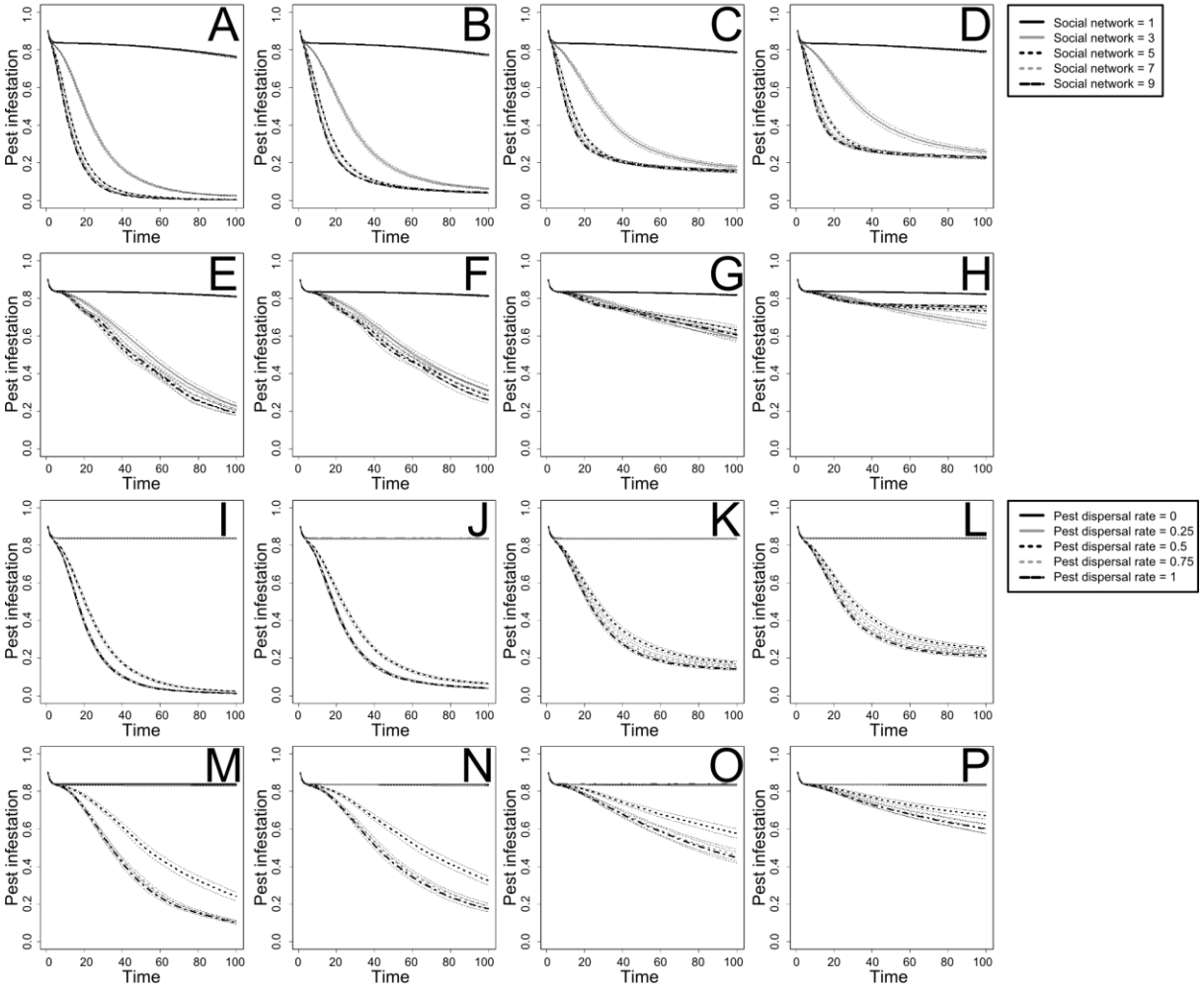


Fig. 3


A
B
C
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G
H
I
J
K
L
M
N
O
P
Pest infestation
Time
Social network = 1
Social network = 3
Social network = 5
Social network = 7
Social network = 9
Pest dispersal rate = 0
Pest dispersal rate = 0.25
Pest dispersal rate = 0.5
Pest dispersal rate = 0.75
Pest dispersal rate = 1

Fig. 4

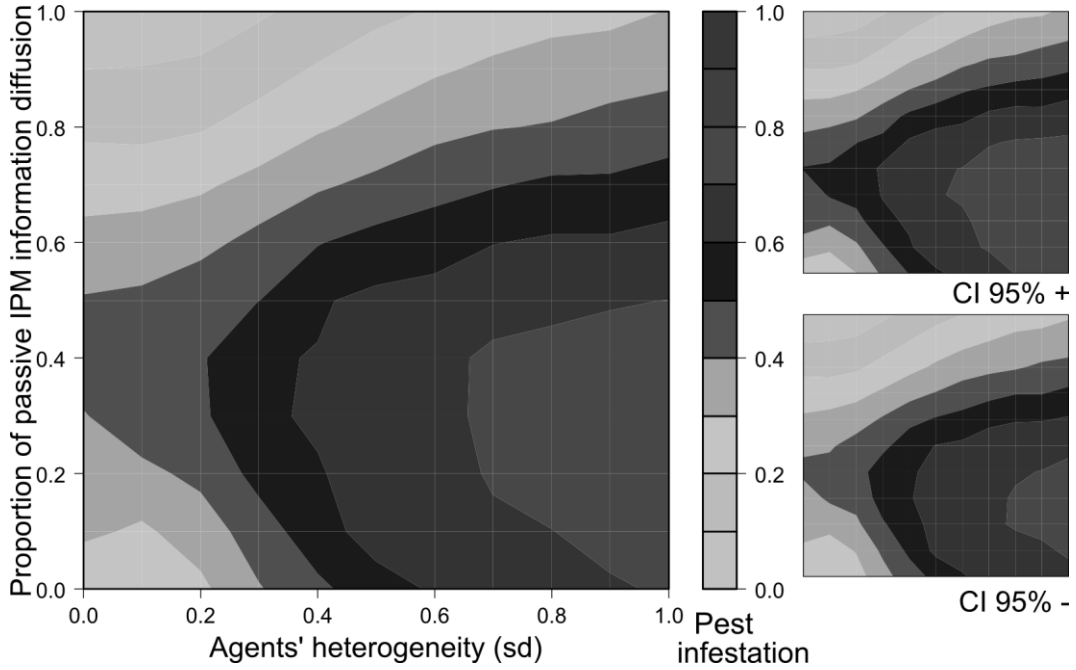
Proportion of passive IPM information diffusion
Agents' heterogeneity (sd)
Pest infestation
CI 95% +
CI 95% -

Fig. 5

2.2. Le couplage d'un modèle de diffusion de l'information avec un modèle de dynamique des populations d'insectes : conséquences pour les agriculteurs dans leur stratégie de contrôle

Résumé en français

Dans le monde entier, la théorie et la pratique de diffusion d'informations agricoles a reposé pendant presque un demi-siècle sur la théorie émise par le sociologue et statisticien Everett Roger de diffusion d'innovations. En particulier, le succès de programmes de diffusion en protection intégrée des cultures dépendrait de l'efficacité avec laquelle l'information se transmet d'agriculteur à agriculteur. Cette hypothèse prend toute son importance lorsque l'on sait que le financement des organisations mettant en place ces programmes repose sur celle-ci. Dans cette étude a été développée une approche innovante grâce à la modélisation à base d'agents combinant un modèle social (théorie de la diffusion d'information) à un modèle biologique (dynamique spatio-temporelle d'un ravageur des cultures), afin d'étudier le rôle de la coopération au sein d'une communauté d'agriculteurs pour le partage d'informations relatives à la protection intégrée des cultures contre un ravageur invasif. Le modèle se base sur des relevés de terrain, incluant les processus d'apprentissage et l'efficacité du contrôle des ravageurs, grâce à des enquêtes réalisées le long de la cordillère des Andes équatoriennes. Les sorties du modèle montrerait que bien que la coopération s'accompagne de coûts à court terme pour les agriculteurs (à titre individuel), elle serait bénéfique sur le long terme en réduisant l'incidence du ravageur pour l'ensemble de la communauté. Cependant, la vitesse restreinte d'apprentissage pénalise la diffusion de l'information qui pourrait être générée au sein d'une communauté d'agriculteurs, conduisant à des délais dans la diffusion et l'adoption des pratiques de protection intégrée des cultures. De plus, les résultats obtenus suggèrent que si les agriculteurs avaient connaissance des bénéfices des mesures prophylactiques à l'encontre des ravageurs invasifs, l'effort initial d'apprentissage pourrait avoir un impact durable sur le long terme. En cohérence avec les modèles traditionnels issus de la théorie de diffusion de l'information, ces résultats montrent comment une approche intégrée combinant les systèmes sociaux et écologiques aiderait à mieux prévoir le succès potentiel des programmes de protection intégrée des cultures. Au-delà de la protection des cultures, cette approche pourrait être applicable à tout programme de gestion d'une ressource ayant comme fondement la diffusion d'innovations au sein d'une population donnée.

Coupled Information Diffusion–Pest Dynamics Models Predict Delayed Benefits of Farmer Cooperation in Pest Management Programs

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Abstract

Worldwide, the theory and practice of agricultural extension system have been dominated for almost half a century by Rogers' "diffusion of innovation theory". In particular, the success of integrated pest management (IPM) extension programs depends on the effectiveness of IPM information diffusion from trained farmers to other farmers, an important assumption which underpins funding from development organizations. Here we developed an innovative approach through an agent-based model (ABM) combining social (diffusion theory) and biological (pest population dynamics) models to study the role of cooperation among small-scale farmers to share IPM information for controlling an invasive pest. The model was implemented with field data, including learning processes and control efficiency, from large scale surveys in the Ecuadorian Andes. Our results predict that although cooperation had short-term costs for individual farmers, it paid in the long run as it decreased pest infestation at the community scale. However, the slow learning process placed restrictions on the knowledge that could be generated within farmer communities over time, giving rise to natural lags in IPM diffusion and applications. We further showed that if individuals learn from others about the benefits of early prevention of new pests, then educational effort may have a sustainable long-run impact. Consistent with models of information diffusion theory, our results demonstrate how an integrated approach combining ecological and social systems would help better predict the success of IPM programs. This approach has potential beyond pest management as it could be applied to any resource management program seeking to spread innovations across populations.

Author Summary

Food security of millions of people in the third world has faced a growing number of challenges in recent years including risks associated with emergent agricultural pests. Worldwide, the promotion of integrated pest management practices has been heavily promoted through participative methodologies relying on farmer cooperation to share pest control information. Recent studies have put into doubt the efficiency of such methodologies evoking our poor knowledge of farmers' perceptions, behavioral heterogeneity, and complex interaction with pest dynamics. While pest management programs have a larger place than ever on the international policy agenda, the debate concerning their efficiency at large scales has remained unresolved. Here, we developed an innovative modeling approach coupling pest control information diffusion and pest population dynamics to study the role of cooperation among farmers to share the information. We found that the slow learning process placed restrictions on the knowledge that could be generated within farmer communities over time, giving rise to natural lags in pest control diffusion and applications. However, our model also predicts that if individuals learn from others about the benefits of early prevention of invasive pests, then a temporary educational effort may have a sustainable long-run impact.

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Introduction

In view of the growing number of challenges related to controlling agricultural pests, the promotion of Integrated Pest Management practices (IPM; a range of methods used for responsible pest control) has a larger place than ever on the international policy agenda [1], [2]. The participation of local communities and other stakeholders in such management processes has long been advocated as an essential step to achieve sustainable development [3]. Over the past decades, extension science has developed many types of participatory approaches towards farmers [4] to promote knowledge of agro-ecological concepts, apply IPM practices, reduce the use of pesticides and improve crop yields [5]. As budget and manpower constraints do generally not allow for direct interaction with every member of the target population, the strategy of most participative IPM programs is to train a limited number of farmers in the community who commit themselves to share the information they learn with other farmers [6]. Following Rogers' "diffusion of innovation theory" [7], the success of extension practices depends on the effectiveness of cooperation among farmers which determines IPM information diffusion from trained farmers (graduate farmers) to other farmers (exposed farmers).

Funding from international development organizations often relies on the important, but poorly studied, assumption that farmers cooperate with their peers, neighbors, or friends [8]. Increasing our understanding of farmers' cooperation theory and practice is a timely issue as field-level interactions among small-scale farmers are increasingly limited in a world of intense social reorganizations associated with land distribution, privatization of ownership, and market-oriented society [9].

A collective action problem that requires farmers to cooperate in information diffusion is exemplified by invasive pest control in fragmented agro-ecosystems [10]. If neighbors of graduate farmers do not adopt IPM measures, then the invasive pests from their fields can re-infest the graduate farmers' fields even if they apply IPM principles [11]. Moreover, in the case of emergent invasive species, farmers cannot rely on preexisting local knowledge, which makes them even more dependent on externally based experience. In farmer communities, IPM for invasive species is therefore characterized by a conflict of interest between individual and group benefit leading to cooperation dilemma [12], [13]. On the one hand, cooperation by graduate farmers to share IPM information is expected, in the end, to benefit the whole community of farmers (including themselves) by an area-wide suppression of the pest. On the other hand, under the assumption that graduate farmers want to prioritize control in their

fields instead of training other farmers, theory predicts that individuals might have little incentive to cooperate and will not contribute to the public good [12]. Both types of behaviors have been classically observed in a wide array of agricultural situations [1]. In the specific case of IPM, farmers' decisions about whether to disseminate or not pest control practices will be closely dependent on pest infestation levels in their own field [1]. This means that farmers' dilemma to train others or not will be tightly linked to pest dynamics at the landscape level, itself depending on landscape characteristics, pest ecology and control behaviors of other famers. Exploring the relative merits of helping others *vs.* self interest in IPM information diffusion therefore requires the coupling of ecological and sociological models, an approach which has, to our knowledge, never been performed in the context of IPM.

The objective of our study was to develop a methodological framework to explore the relevance of participative IPM extension programs for pest control. We carried out these investigations in the context of an IPM program launched to help small scale farmers facing the arrival of an invasive insect pest, the potato tuber moth (*Tecia solanivora* Povolny) in the Ecuadorian Andes [14]. This region was highly relevant for our study as there is a long history of social reciprocity in the Andes that extends to pre-Incan times and has been one of the keystones for why farmers have been able to successfully farm for centuries in such harsh conditions [15]. We then built an agent-based model (ABM, [16], [17]) merging a spatially explicit pest population dynamic model through a cellular automaton (CA) with a field-based multi-agent system describing farmer features and behaviors (Fig. 1A). The global output of our ABM was determined from pest–landscape interactions, pest-farmer interactions, and inter-farmer interactions. To mimic real-world patterns of farmer behaviors as closely as possible, our ABM was implemented with field data, including learning processes and control efficiency, from large scale surveys from c.a. 300 farmer households in the Ecuadorian Andes. In our model, the agricultural landscape was modeled as a lattice composed of cells that represented various land plots of groups of farmers (hereafter named agents) within the same community (in total, 6 neighbor agents in the same community representing about 220 people, Fig. 1B). Pest dynamics was driven by the intrinsic population growth, migration, and pest control practiced by agents depending on their IPM knowledge. Under our IPM program, one agent was trained to control pest infestation in his fields. In return, this graduate agent was required to diffuse the IPM information to other agents so that they can increase their IPM knowledge and implement efficient practices. Agent decision to diffuse the information to others mainly depended on pest infestation level in his fields but also on social and economic factors included in the diffusion process of IPM information among farmers.

Therefore, pest control at the community level was modeled as emerging from IPM information acquired by one graduate agent and spreading through exposed agents (see Text S1).

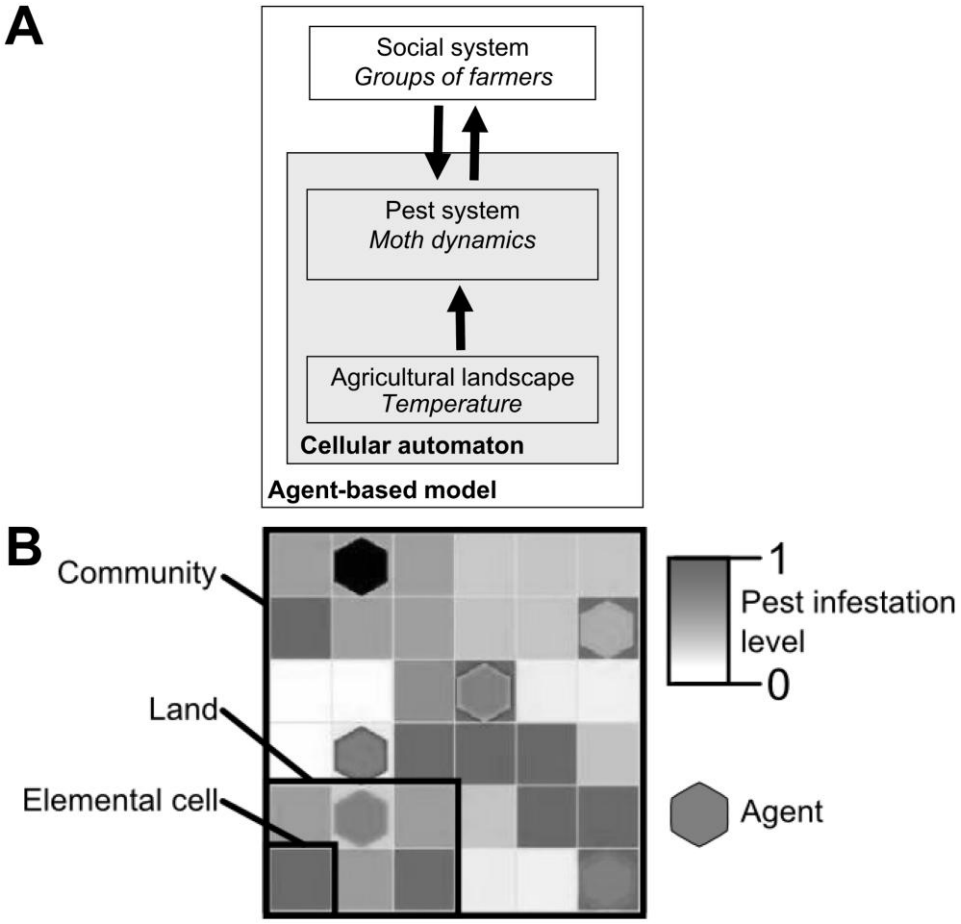

Figure 1. Model schematization. A. The cellular automaton (pest population dynamics sub-model driven by temperature) is coupled to an agent-based model, made by agents controlling the pest and exchanging pest management information as a function of infestation levels in their land. B. Representation of the model where the community consists of 36 cells, divided into 6 lands of 6 elemental cells. Each cell sizes 500×500 m. One agent (represented by an hexagon) is assigned to each land. The green gradient indicates pest infestation level, from no presence in white to the carrying capacity of each cell in dark green. Each agent interacts both with pest (control) and other agents of their community (pest management information exchange).

We believe that the relevance of our study stands in two main points. First, recent works on collective actions of IPM diffusion have reported that because behaviors and perceptions towards new information and technology can vary widely among farmers,

farmers' behavioral heterogeneity is a key issue to understand and predict the success of pest control information diffusion throughout the community, and therefore the success of the IPM program at a large scale [14], [18]. In this context, ABMs may reveal ideal tools to better understand and predict the sustainable development of farmers' control practices [19]–[21] as they allow simulating the actions and interactions of autonomous agents (either individual or collective entities such as organizations or groups of farmers) with a view to assessing their effects on the system as a whole. Using ABM therefore allows integrating behavioral complexity of farmers and performing theoretical experiments (*e.g.*, varying the level of farmer cooperation) which could not be performed in the real world (for time, ethical or financial reasons). Although ABM have increasingly been applied to physical, biological, medical, social, and economic problems [22], [23], [16] it has been, to our knowledge, completely disregarded by IPM theory and practice. Second, our study proposes an innovative computational framework merging recent advances in contagion-like model of knowledge diffusion through human populations [24], [25] and coupled land management models with spatially explicit species spread models (see papers presented at LandMod 2010 or Global Land Project 2010). Such a framework combining two approaches which developed in relative independence likely has potential beyond pest management as it could be applied to any resource management program seeking to spread innovations across populations.

Results

The field survey revealed that, at the beginning of our program, a majority of farmers (87%) had a low IPM knowledge (score ranging between 0 and 2) regarding potato moth control (Fig. 2A). Our data further showed that although this knowledge could be greatly increased through training (graduate farmers reached an IPM knowledge of 4.39±0.61), those skills were not easily diffused to exposed farmers by informal training sessions (Fig. 2B). After having graduate farmers shared information with exposed farmers the mean knowledge score of the 64 surveyed exposed farmers increased only slightly when compared to control, from 0.96±0.80 to 1.65±0.53 (Student t-test, $t = -1.717$, $P = 0.111$). Interestingly, although moth control gradually increased with increasing IPM knowledge scores (linear model fit, $R2 = 0.51$, $P<0.001$), there were a few cases in which farmers with relatively high IPM knowledge had also poorly efficient pest control in their fields, probably due to contamination from neighboring fields (Fig. 2C).

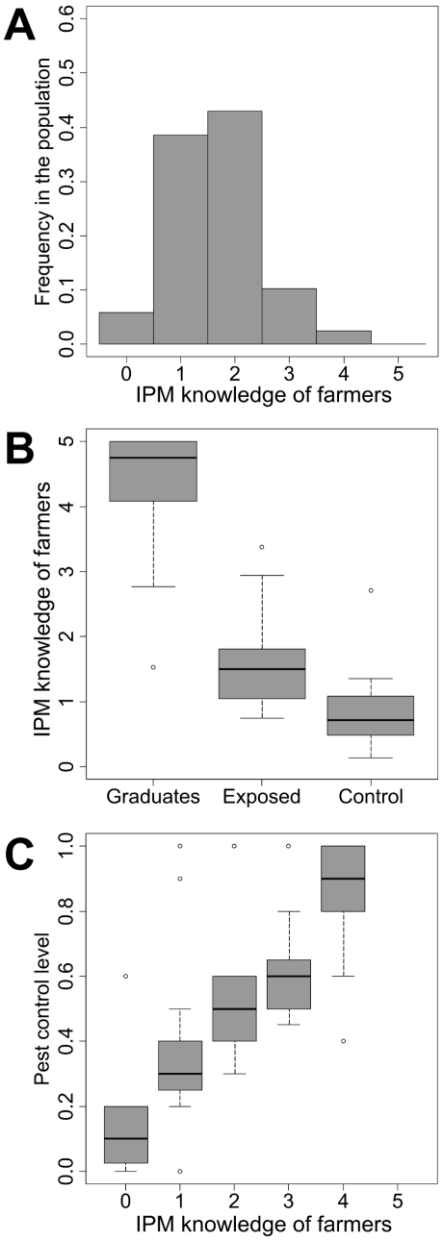

Figure 2. Field data. A. Distribution of IPM knowledge of farmers (n = 293 inquests) B. Efficiency of learning process between graduates and exposed farmers (n = 85). C. Relationship between IPM knowledge of farmers and pest control (n = 83 households) (linear model; $R^2 = 0.51$, $P<0.001$).

Once the ABM was set up with these real-world data, we explored on a 20-year time scale the influence of the level of cooperation among agents (*i.e.* how often graduate agents did share their information with others) on pest infestation levels. Our model predicted that knowledge acquisition by exposed agents would follow a logistic regression through time ($R2 = 0.50 \pm 0.11$, $P<0.05$, Fig. 3A). Our simulations further predicted that both IPM knowledge diffusion and spillover after training would significantly decrease moth infestation by 60 to 70% from their initial levels (Fig. 3B). Time dedicated by graduate agents to train exposed agents instead of controlling pest had the short term consequence of increasing pest infestation in his own land (interviews with farmers revealed that training others would demand time and compromise of coordination with consequences in terms of pest control in their own field.). However, as exposed agents were being trained, graduate agents were less solicited thereby being able to dedicate more time to pest control. Importantly, the patterns of IPM information diffusion among agents predicted by our ABM was consistent with the Bass model (F-test, $P<0.001$, Fig. 4), a model traditionally used in diffusion of innovations [24]. The ability of our ABM to reproduce Bass model predictions therefore provided a validation of the correctness of information adoption patterns among agents, mainly through internal ("word-of-mouth") influences.

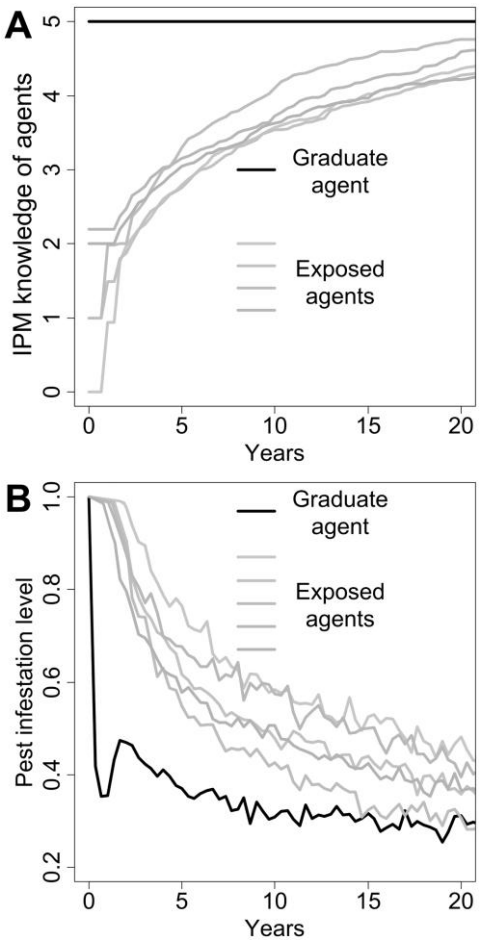

Figure 3. Results of ABM simulations. ABM results showing the evolution of IPM knowledge of agents (A) and pest infestation level (B) through time (mean of 100 simulations).

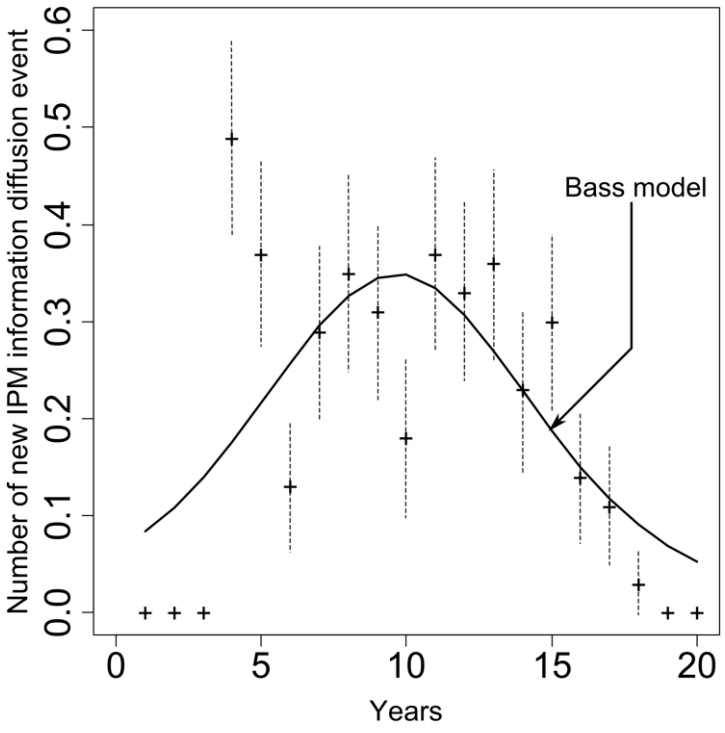

Figure 4. Number of new IPM information diffusion event over time fitted to the Bass model. The fit was obtained following [47] ($p = 0.015 \pm 0.001$, $P<0.001$; $q = 0.296 \pm 0.011$, for all parameters $t \geq 12.67$, $P<0.001$). Each point is the mean of 100 repetitions with confidence intervals 95% in dashed lines. The theoretical prediction curve represents the derivative of N over time.

Results of our simulation of the effect of farmer's cooperation level on pest control showed that within the first 6–7 years, pest infestation levels in both graduate and exposed agents' lands remained higher than those expected in the lands of a non-cooperating agent, whatever the cooperation levels. After 6–7 years, cooperating graduate agents had lower pest infestation level than non-cooperating ones, and therefore received the benefit of cooperating. Finally, for high levels of cooperation among agents (>0.5), our model predicted that after 6–7 years, pest infestation levels at the scale of the entire community (*i.e.* in all lands of agents) would be lower than levels expected in the fields of a non-cooperating graduate agent. The benefit of cooperation had therefore scaled up at the level of the whole community of agents (Fig. 5).

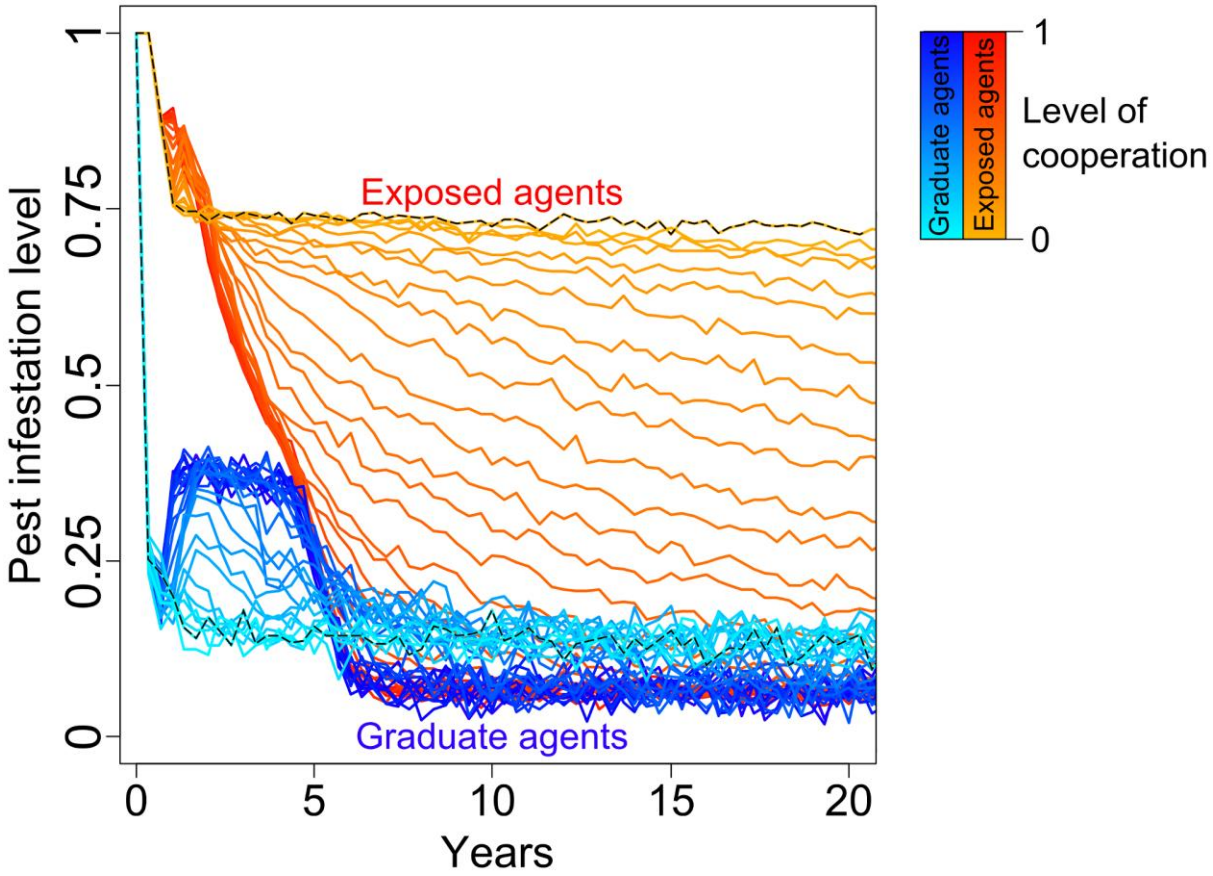

Figure 5. Influence of cooperation among agents on pest infestation in fields of exposed (red) and graduate (blue) agents.

Discussion

Since the emergence of the concept of knowledge based economy [26], the analysis of information diffusion has become a key issue to organization research [27]. Our results showed that the slow IPM learning process measured in Andean farmer communities placed restrictions on the amount of information that could be diffused within the community over time, giving rise to natural lags in IPM applications. This reinforces the view that IPM outcome at the community level will be achieved on a relatively long-term scale for the farmer, a feature which may be common to many agriculture programs. In an influential study that spawned an enormous diffusion of literature in rural sociology, [28], estimated that it took 14 years before hybrid seed corn was completely adopted in two Iowa communities. Rogers [7] also reported slow adoption in crop protection management in the Colombian Andes and Berger [21] showed that behavioral heterogeneity among Chilean farmers, delayed for almost 10 years the use of new irrigation methods. In our study, the six year delay in benefits of cooperation was mainly due to the limited spread of IPM information from graduate to exposed farmers which itself may have been a consequence of high IPM knowledge heterogeneity among farmers. Information is indeed expected to flow less smoothly in a heterogeneous population, particularly when the performance of new practices is sensitive to imperfectly transmitted information [29].

Our simulations also showed that there were short-term costs for the diffusion of IPM information resulting from our assumption that farmers cannot control pests in their own fields when they share IMP information with other farmers. Indeed, “lack of time” is a common motive invoked by farmers when they are questioned why they do not share IPM practices they learned with neighboring farmers [30]. As farmers often believe that there is a trade-off between diffusing and practicing IPM information, we think that an important outcome of our study was to show that, even if such a trade-off is included in the model, cooperating farmers would still benefit from IPM information diffusion in the long run. It is also likely that, in some cases, farmers may practice and diffuse new information simultaneously [1]. Cooperating farmers would then not suffer from short-term costs, potentially increasing their cooperation will, thereby speeding up information transfer throughout the community.

Obviously, our modeling approach made a series of simplifications which may be important to consider. For example, farmers usually tend to make high contributions initially but over time contributions dwindle to low levels. Many people are conditional cooperators,

who in principle are willing to cooperate if others do so as well, but get frustrated if others do not pull their weight [31]. In agricultural systems personal networks, where trusted people (prestigious individuals, people of authority or holding otherwise vested power and influence) often play a key role in decision making, are difficult to integrate into models due to their dynamic, multi-directional, and non-symmetric nature [32]. Moreover the spread of behaviors may arise from the spread of social norms or from other psychosocial processes, such as various types of innate mimicry [33]. A recent study has shown that cooperative behaviors can cascade in human social networks even when people interact with strangers or when reciprocity is not possible; people simply mimic the behavior they observe, and this mimicking can cause behaviors to spread from person to person to person [34]. In this case, the rate of diffusion is largely dependent upon the knowledge (*i.e.*, relative advantage, compatibility within the social setting, observability, and simplicity). Finally, another limitation may arise from the use of a behavioral reciprocity model. Theoretically, the adoption of IPM cooperative behavior among farmers could be favored as the reciprocated benefit outweighed the immediate cost [27]. However, in practice, the delay between the cost of a cooperative act and the benefit of reciprocated cooperation (from 7 to 20 years for graduate agents in our study) would introduce a number of cognitive challenges. For example, temporal discounting (for example devaluing of future rewards in the case of shift in crop type produced), often results in a preference for smaller, immediate rewards over larger, delayed rewards [35]. Variation in human discounting and cooperation validate the view that a preference for immediate rewards may inhibit reciprocity [35].

Despite these limits the ability of our model to capture real-world patterns of pest control (Fig. S5 in Text S1) and information diffusion (Fig. 4) indicates that our findings may yield important insights for IPM science and policies. First, IPM programs worldwide are confronting the reality of increasingly subdivided habitats managed as smaller areas, reducing the likelihood that pest population will be controlled, thereby requiring higher levels of cooperation among farmers [10]. We showed that when farmers make control decisions based on lower levels of damages occurring on their own land, they can increase information spread and the speed with which the whole community can control pest populations. Second, our study stresses the need to develop a comprehensive and empirically-based framework for linking the social and ecological disciplines across space and time [19]. In our model, predictions of the coupled dynamic of pests and farmer behavior show the evidence that farmer to farmer training can help the broader community control pest infestation in the long term. Third, as institutions increasingly seek to help communities sustainably providing local

public goods themselves rather than depend on external assistance, the idea that development projects should aim at financial sustainability through local cooperative actions has had tremendous influence on funders. Our study shows that sustainable approaches to providing local public goods concerning invasive pest control would be possible despite a challenging delay between the cost of a communal act and the benefit of reciprocated cooperation. However, if individuals learn from others about the benefits of early prevention of invasive pests (*i.e.* cooperation takes from low levels of pest populations), then a temporary educational effort may have a sustainable long-run impact.

Materials and Methods

Study area

We addressed the issue of the importance of farmer cooperation in invasive pest management in the socio-agricultural system of the Ecuadorian highlands where potatoes (Solanum tuberosum L), are a major staple [36]. In 1996 a new pest, *T. solanivora*, invaded the country attacking potato tubers in the field and in storage and becoming one of the most damaging crop pests in the region [37]. Under the climatic conditions of the Ecuadorian highlands (sierra) potatoes are grown at any time of the year between elevations of 2400 m and 3800 m elevation [38]. The agricultural landscape of the highlands is made up of a mosaic of small potato fields (<1 ha) at various stages of maturation in which potato moths are active all year round. IPM programs have been implemented for about 10 years by the INIAP (Ecuador's National Institute for Agronomy Research) and the CIP (International Potato Center), through the Farmer Field School methodology [39]. In the North Andean region, collaborative work in the form of “mingas” and “Aynis” is necessary among small groups of farmers in order to realize hard tasks like sowing or harvesting. These labor force exchanges, despite of being very hierarchical, share common practices [40]–[42].

Model overview

We built a representation of socio-agronomical landscapes of the central Andes at an altitude of 3000 m, which corresponds to the zone where most farmers cultivate potato. This landscape comprised three key elements: the socio-agricultural landscape, the potato moth population, and the groups of farmers (Fig. 1B). First, characteristics of the socio-agricultural landscape were set up using data from published field surveys: 1) the median community size in the study area was about 150 people [14] which roughly corresponded to 6 household units

(*i.e.* a group of fields cultivated by one group of farmers). 2) The size of elemental cells was set up to 500 m×500 m in order to accurately model pest dispersion among cells with regards to insect's flight capability [43]. 3) Seasonal variability in climatic features (both temperature and rainfall) for each cell was obtained using the Worldclim data set [44].

Second, potato moth dynamics were simulated through a cellular automaton (CA) recently developed by our team [43]. Briefly, the CA is spatially explicit, stage-structured, and based on biological and ecological rules derived from field and laboratory data for *T. solanivora*'s physiological responses to climate (temperature and rainfall). Main processes include moth survival (climate dependent), dispersal to neighbor cells through diffusion processes (density dependent), and reproduction (climate dependent) (see Fig. S1 in Text S1). In each time step (equivalent to one moth generation, about 2 months) the infestation grows and spread over household units. A Mathematical presentation of the underlying principles of the pest model, along with general results identifying the important simulation details and their consequences, are given in [45].

Third, to transfer the pest model into an ABM we populated the agricultural landscape with artificial agents acting individually upon pest dynamics (see Fig. 1A and Appendix for a complete description of the model structure). Briefly, each agent represented a group of farmers and was set with a behavioral model that guided his or her decisions. Potato moth control at the community level was modeled as emerging from IPM information spreading through agents that composed the community. The ability to learn IPM recommendations was considered as an adaptive trait that indirectly contributed to agent's fitness by improving their capability of controlling pest populations (and therefore assuring their crop production). Agents with different IPM knowledge interacted directly with each other to exchange information (agents with less information learned from other agents). We used a reciprocity model for cooperation in which agents paid a short term cost of cooperation for the future benefit of a community member's reciprocated cooperation [35]. Agents indeed perform multiple roles which constrict the amount of time and energy they may allot to any single activity. They perceived and controlled pest infestation levels in their field depending on their IPM knowledge (see below and Protocol S1, S2).

Setting up agent behavior rules with field survey data

To explore the profitability of our IPM program as a function of the coupled dynamics of agent behaviors (and learning spillover) and pest population, we needed three pieces of field information: 1) the initial IPM knowledge of each agent in the community, 2) the relationship between IPM knowledge and pest control, and 3) the efficiency of IPM

information diffusion between graduate and exposed agents (including a wide range of social factors influencing innovation diffusion). We acquired these data through a farm-level empirical survey from nationally representative samples of farmers in rural Highland Ecuador. Our database was obtained through a three-year household survey conducted in 2006–2008 in four provinces of the Ecuadorian highlands (Bolivar, Tungurahua, Cotopaxi, and Chimborazo) using standard household survey techniques [46]. Survey zones had not been covered by any educational program regarding potato moth management. In total, 293 potato grower families from about 100 different communities were interviewed, gathering data on IPM knowledge in communities and pest control. The efficiency of IPM learning and dissemination processes was assessed through farmer field schools as described in details by [30]. Briefly in each target community, we first performed a baseline study of IPM knowledge for as many community members as possible. Farmers interested in IPM extension were then trained through FFS procedures during eight one-day sessions over the duration of potato crop cycle (about 4 months). Each graduate farmer committed himself in training at least five other farmers. Informal discussion with trained framers revealed that the amount of time they dedicated in training other farmers varied greatly, between several hours to several days. Exposed farmers were then interviewed to measure their IPM knowledge and the efficiency of the IPM information diffusion process.

Cooperation rules among agents and ABM simulations

In each community, the IPM knowledge of agents were set up according to the frequency distribution presented in Fig. 2A (one agent with a score of 0, two with a score of 1, two with a score of 2, and one with a score of 3). We then increased the knowledge of the agent with a score of 3 to a score of 5 as if it had participated in a FFS (see Fig. 2B). This agent became the graduate agent of the community. According to FFS recommendations, this agent (in the case he or she was eager to cooperate) shared his information with exposed agents of his community (defined as an agent with a lower IPM knowledge). Once other exposed agents achieved, in turn, a higher IPM knowledge, they could also share their information with neighbor agents. An agent could share information with only one agent with a lower IPM knowledge (during this time the farmer could not control pest in his fields). When not sharing their information each agent was able to control pest in his field with an efficiency which depended on their IPM knowledge (following Fig. 2C). Again, the pest level in each cell was driven by both intrinsic population growth and diffusion from neighbor cells (see above).

Once the ABM was set up and sensitivity analysis performed (Fig. S2–S4 in Text S1), we further explored how agents' level of cooperation (*i.e.* how available agents were to share their information with others) would influence the benefits of our IPM program at both individual farmer and community levels. Because decision of poor farmers to cooperate for crop protection is likely to be driven by self-interest rather than altruism [14], [15], we assumed that farmers would be more prone to cooperate in IPM information diffusion when they perceive that a pest represents a danger for themselves. In our model, varying levels of cooperation were obtained by changing the pest infestation level that triggered a control action by agents (see Text S1). Each simulation was repeated 100 times over 120 time steps (*i.e.* about 20 years) and pest infestation levels were given for exposed agents, graduate agents, and the whole farmer community.

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Author contributions

Conceived and designed the experiments: FR OD. Performed the experiments: FR OD. Analyzed the data: FR OD. Contributed reagents/materials/analysis tools: FR OD. Wrote the paper: FR OD.

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CHAPITRE 3 -

LA MODELISATION COMME OUTIL DE FORMATION ET DE COMMUNICATION

Chapitre 3 - La modélisation comme outil de formation et de communication

Dans le chapitre précédent, le couplage entre modèles de différentes disciplines a contribué à mettre en évidence la modélisation comme support intégratif du travail pluridisciplinaire, particulièrement au moyen de la modélisation agent-centrée. Ce travail a par ailleurs démontré l'importance de la prise en compte des comportements humains dans toute leur hétérogénéité pour une meilleure compréhension de la dynamique spatio-temporelle d'insectes ravageurs des cultures. De ce constat et d'un travail participatif préliminaire avec une communauté d'agriculteurs, l'auteur a cherché à utiliser les modèles précédemment décrits comme support de formation pour les techniciens comme les agriculteurs des pays où cette étude a été menée.

La contribution de l'auteur au travail de recherche participative a été mineure et l'article publié dans la revue *Ambio* aurait pu figurer en annexe, mais compte tenu de sa pertinence dans les orientations qu'il a donné à ce manuscrit (le lecteur y trouvera de précieuses informations pour appréhender les systèmes socio-écologiques agricoles nord andins), l'auteur a choisi de le faire figurer dans le corps de ce manuscrit.

Le travail de formation a donné lieu à un article scientifique publié dans la revue *Journal of Artificial Societies and Social Simulation.*

Ce sont ces deux articles qui constituent le troisième chapitre de ce manuscrit de thèse dont voici les citations :

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

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

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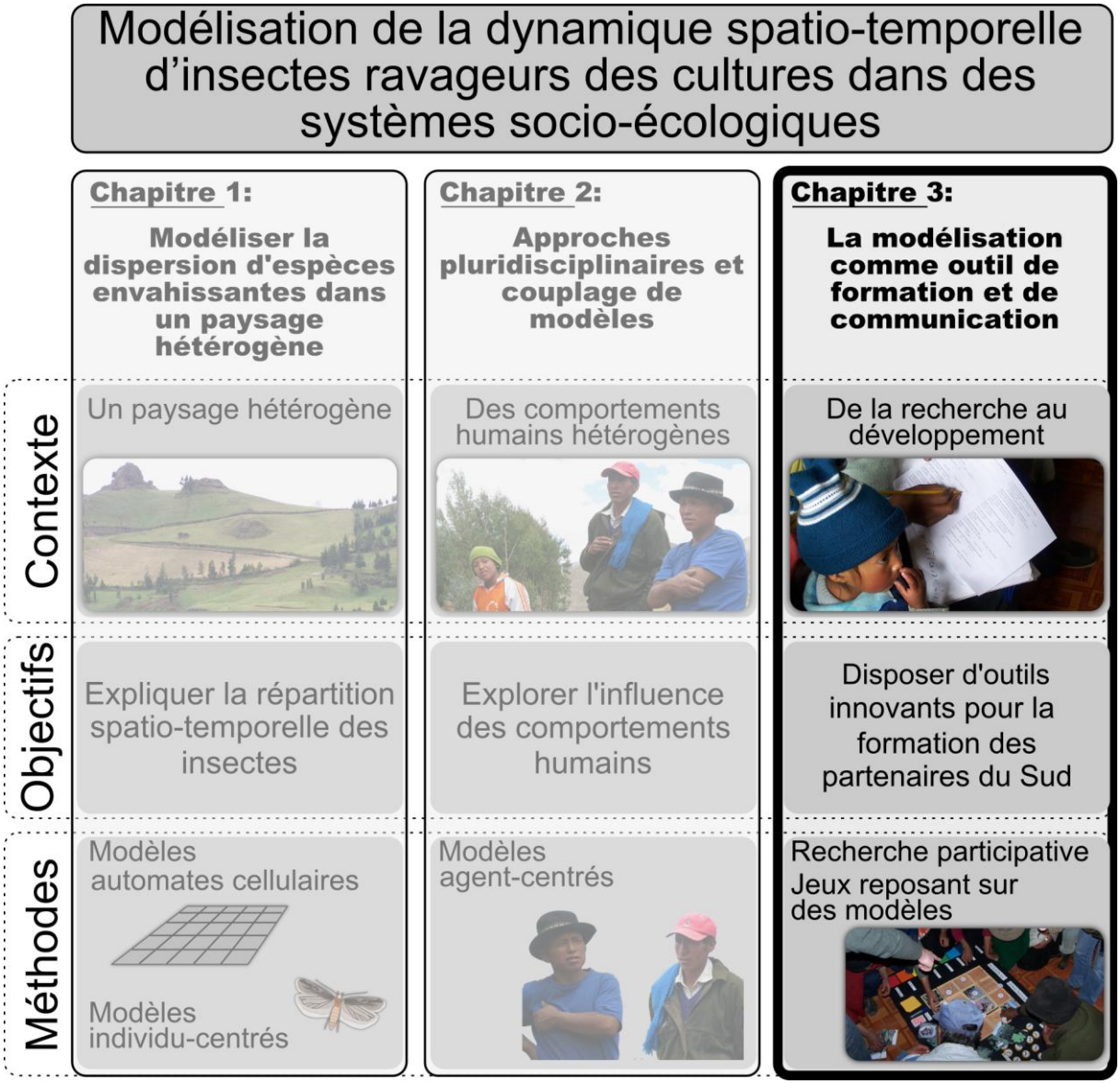

3.1. Quand la recherche participative aide les agriculteurs et les scientifiques à contrôler des ravageurs envahissants dans les Andes Equatoriennes

Résumé en français

La recherche participative n'a pas été beaucoup employée dans les pays en voie de développement pour étudier les ravageurs des cultures envahissants, ces derniers représentant pourtant un frein croissant au développement durable sous les tropiques. Cette étude présente un système de surveillance des populations de ravageurs par une communauté d'agriculteurs, et se concentre sur trois espèces envahissantes de teignes de la pomme de terre. Le réseau de surveillance a été développé et mis en œuvre par de jeunes agriculteurs dans une zone montagneuse isolée, en Equateur. Les participants locaux ont rassemblé des données du front d'invasion des teignes, ce qui a permis de mettre clairement en évidence la relation existante entre l'abondance d'une des espèces (*Tecia solanivora*) et l'éloignement au marché principal. Cette relation suggère que les mécanismes structurant les populations envahissantes au front d'invasion diffèrent de ceux existants chez les populations installées de longue date. Le réseau de surveillance participatif avec les populations locales pourrait en conséquence servir de premier système d'alerte pour détecter et contrôler les nouvelles espèces envahissantes de ravageurs dans des pays où la gestion quotidienne des ressources biologiques est en grande partie entre les mains des habitants des zones rurales à faibles revenus.

Community-Based Participatory Research Helps Farmers and Scientists to Manage Invasive Pests in the Ecuadorian Andes

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Abstract

Participatory research has not been a conspicuous methodology in developing nations for studying invasive pests, an increasing threat to the sustainable development in the tropics. Our study presents a community-based monitoring system that focuses on three invasive potato tuber moth species (PTM). The monitoring was developed and implemented by young farmers in a remote mountainous area of Ecuador. Local participants collected data from the PTM invasion front, which revealed clear connection between the abundance of one of the species (*Tecia solanivora*) and the remoteness to the main market place. This suggests that mechanisms structuring invasive populations at the invasion front are different from those occurring in areas invaded for longer period. Participatory monitoring with local people may serve as a cost-effective early warning system to detect and control incipient invasive pest species in countries where the daily management of biological resources is largely in the hands of poor rural people.

Keywords: Insect pest - Developing countries - Participative monitoring - Farmer communities - Education - Andes

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Introduction

Community-based participatory research involves a partnership between researchers and community members who collaborate on a research project to address social and environmental problems (Stoecker 2001; Wallerstein and Duran 2003). Unlike conventional research, community-based investigations are tied to the participation of community groups who have interest in applying the research findings to improve their quality of life (Jacobson *et al.* 2006). Over the past 10 years, an increasing number of conservation programs have involved native people to meet the twin goals of sustaining local livelihoods while simultaneously protecting the structure and function of the environment within which their community and culture are imbedded (Agrawal and Gibson 1999; Ambrose-Oji *et al.* 2002). Examples of environmental issues addressed by community-based research include the monitoring of water quality in the Philippines (UN Department of Economic and Social Affairs 2003), the testing of fishing methods to protect undersize fish in Benin (Afrol News 2003) and the monitoring of biodiversity in protected reef areas (Hill 2004). Community-based conservation has been particularly successful in developing countries where the daily management of biological resources is largely in the hands of poor rural people and local government staff with virtually no operational funding.

Community-based monitoring has therefore become widespread in the last few years, documenting many outcomes related to biological resource management (see Calheiros *et al.* 2000; Olsson and Folke 2001; Curtin 2002; Lawrence 2002; Danielsen *et al.* 2005 and related articles in the same issue). Surprisingly, community-based monitoring has not been a conspicuous focus for invasive pest species in developing nations, an increasing threat to the sustainable development in the tropics. Strategies to manage invasive species have been well implemented in developed countries (for example, "weed-watcher" groups have been collecting data on the distribution of invasive plant species in the United States; Mehrhoff *et al.* 2003). Although unpublished initiatives of invasive species management have been developed in a few third world countries, these nations have far fewer tools to face this global issue (Borgerhoff Mulder and Coppolillo 2005). Pest species that have become invasive contribute to exacerbating vulnerability of local communities and in some cases foreclosing livelihood and development options, especially when food security is at risk (Lockwood *et al.* 2007). Poverty, along with inequity, particularly in trade and access to technology make invasive pest monitoring programs particularly timely and challenging for developing countries. Monitoring programs are an important component of good environmental

governance as they ensure that emergent threats are identified and addressed (Lovett *et al.* 2007).

Within the last 30 years, three species of potato tuber moths (PTM, Lepidoptera: Gelechiidae), *Phthorimaea operculella* (Zeller), *Tecia solanivora* (Povolny), and *Symmetrischema tangolias* (Gyen), have been assembled in combination of two of three species into the potato fields of the Northern Andes of Venezuela, Colombia, Ecuador, Peru, and Bolivia through successive introductions from different origins. *T. solanivora* was first described from Guatemala (Povolny 1973) and introduced to South America (Venezuela) via highly infested potato seeds imported from Costa Rica (Puillandre *et al.* 2008). It has then reached Colombia in 1985 and Ecuador in 1996. The invasion history of *P. operculella* and *S. tangolias* in Ecuador is far less clear but it is probable that they were sequentially introduced from Peru in the 1980's and 2001, respectively (Herrera 1998; Dangles *et al.* 2008). These putative different dates of introduction do not necessary mean that the three PTM species are in different phase of their invasion history. The three species indeed show singular population dynamics (Dangles *et al.* 2008) and complex inter-specific interactions (Dangles *et al.* 2009), which challenge our understanding of their spread in the country. It is, however, known that 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 three pest species in all parts of Ecuador. At the larval stage, the three PTM species share the same resource, the potato Solanum tuberosum L. (Solanaceae), itself widespread between altitudes of 2400 and 3800 m a.s.l. In the highlands of Ecuador, potatoes are a major staple, and more than 90000 producers grow them on about 60000 ha of land (Pumisacho and Sherwood 2002). This complex of species represents one of the most serious agricultural pest problems in the Northern Andes with an estimated loss of 150 million dollars per year, principally in the poorest regions of Central Ecuador (Palacios *et al.* 2002; Pollet *et al.* 2003). In addition to threatening food security in the Northern Andes, these invasive species are a potential threat for wild Solanaceae found in the páramos (high-altitude tropical grasslands with high biodiversity and endemism), a threat facilitated by the rapid upward expansion of the agricultural frontier (Gondard and Mazurek 2001).

We had anecdotal evidence that local farmers facing this problem in different regions were willing to be involved in studying these invasive pests because they saw new "moth-like pests" in their field and also declines in potato production—although it was not clear whether the two factors were correlated. This participatory monitoring effort was developed in response to farmers' willingness to participate in the research, as well as a mutual desire

among local people and scientists to quantify risk levels associated with PTM as a means of improving livelihoods in poor and remote regions of Ecuador. By accessing research at multiple levels (see Abay *et al.* 2008), this participatory study followed the traditional research process (objective definition, sampling, data analysis, discussion; see Stoecker 2002) but with the community involved at each step of the process. Some more complex data analysis was done by researchers, but the bulk of interpretation occurred with the involvement of community members (see below for further description). The overall goal of this study, which combines participative, scientific, and educational aspects, is to document how a community monitoring project can provide useful insights for invasive pest management in poor and remote tropical regions.

Methods

Study Site and Farmer Communities

The study area was located in the central Ecuadorian province of Bolivar, canton of Guaranda, parish of Simiatug (Fig. 1). This parish comprised roughly 45 Kichwa communities living between 2800 and 4250 m of altitude, that share similar characteristics in terms of social organization, date of establishment, and agricultural practices (Culqui 2005). With about 1200 inhabitants, Simiatug is the economic center of the valley, and the communities outside Simiatug are smaller in size and density (50–700 inhabitants; see Table 1). Currently, about 25000 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 (mainly the native varieties "Tulca," "Uvilla" and the commercial variety "Gabriela") as well as cattle and sheep. In 2005, only 2.9% of the potato production was commercialized outside Simiatug (Culqui 2005) thereby potentially limiting PTM introduction in the valley. The deteriorated road network together with the landscape configuration of the valley (squeezed between large areas of natural páramos; see Fig. 1) likely protected, to some extent, Simiatug communities from pest invasion. The rehabilitation of the road sections from Guaranda northward to Salinas was completed in 2006, and commercial exchanges from and to Simiatug are currently increasing as is the risk of PTM introduction. Because of the emerging threat from PTM, local farmers were interested in quantifying the densities of PTM species in the Simiatug valley, and to learn about potential risks associated with PTM and how to control them. This latter point was particularly important due to the low level of education in the communities: only 3% of the population has

received formal training in insect pest management (Culqui 2005; Dangles and Carpio, unpubl. data).

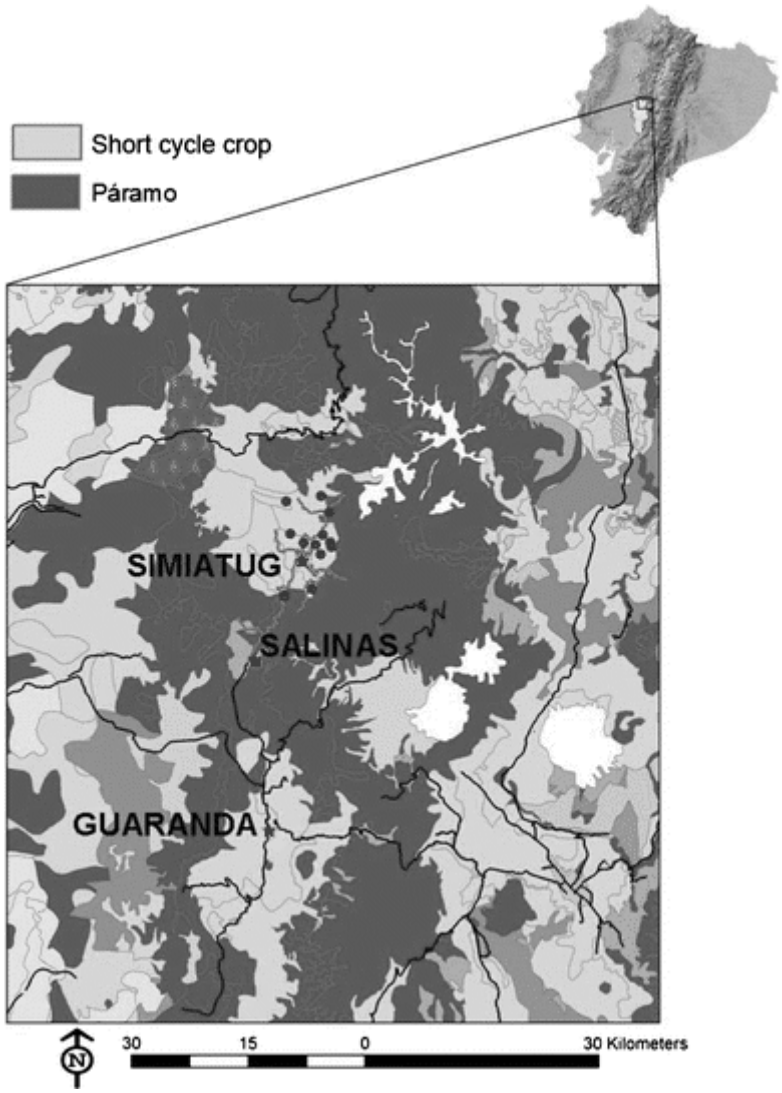

Fig. 1 Map of region of Simiatug (Bolivar, Ecuador) showing the location of the 13 villages (blue dots) involved in the participative monitoring. The figure also presents road network (black lines) and land use (páramos, some high altitude grasslands and short cycle crops such as potatoes)

Table 1 Characteristics of the communities that participated in the PTM monitoring over the study period (October–December 2006)

Communities	Altitude (m)	Mean temperature (°C)	Rainfall (mm)	Main potato variety cultivated	Village size	Remoteness index
Simiatug	3300	12.8	133	Gabriela	3000	0.0
Yanaquero	3525	12.9	136	Tulca	50	0.15
Pambugloma	3075	13.2	102	Gabriela	100	0.08
Rayo Pamba	3725	11.1	145	Rosita	250	0.03
Jabas Pucho	3500	11.4	130	Tulca	700	0.05
Papaloma	3328	12.9	141	Rosita	300	0.05
Calvario	3225	13.1	127	Gabriela	250	0.05
Durazno	2750	15.5	107	Gabriela	100	0.04
Cascarrilla Grande	2555	16.2	124	Gabriela	600	0.2
Zuma Chupa	3150	13.0	111	Tulca	100	0.23
Pimbalo	3625	11.0	137	Rosita	300	0.05
Yuropacha	3750	10.9	143	Rosita	100	0.03
Tibulo	3400	12.5	137	Gabriela	100	0.05

All data have been acquired from community members except precipitations. Mean precipitation data for each site during the study period was interpolated from meteorological stations data using the Worldclim layers available in the geographical information system (GIS) software Arcview 9.1

First Session: Negotiation of Research Objectives and Processes

In order to attract local stakeholder participants and insure that research was driven by their interests, the objectives and process of the participatory research were developed together with farmers from Simiatug during a preliminary negotiation session. The farmers were neither paid nor given food or things (clothes, books) to enhance participation. At the beginning of the session, there was a consensus among farmers about the need of implementing a pest management program in their valley. Together with freeze, pests were indeed the most important problem putting at rick their crops, especially potatoes. The negotiation continued over the questions of process and practical outcomes of the program.

Two main issues were outlined by the farmers: (1) their willingness of the involvement of young people from their community and (2) the need of practical results to control the pest at the end of the participatory research. From our part, we stressed the need of establishing a monitoring of PTM abundance and damages potato to quantify the extant of the problem in the valley. Based on these discussions, the following short-term objectives were established: (1) to monitor and analyze the abundance and distribution of PTM and damages to potatoes in storage with the help of young people from the community and (2) to propose solutions for effective control. Long-term objectives were to strengthen the local economy through integrated management of insect pests and decrease the risk of potato production collapse. Though lengthy, we think that this negotiation phase was important to build trust with farmers and to produce research conclusions that would be more relevant and more likely to be implemented by the community.

Second Session: Training and Monitoring

Thanks to the authorities of the College of Agriculture of Simiatug, 13 young farmers (age ranging from 17 to 25, 11 men, 2 women) were identified to be part of participatory monitoring of PTM abundances. In agreement with decisions taken during the negotiation session, farmers were selected so that the monitoring could include spatially dispersed communities allowing a relevant estimation of PTM distribution in the valley. Consequently, the 13 farmers belonged to 13 different Kichwa communities located at various altitudes and distances from Simiatug (see blue dots in Fig. 1; Table 1). In order to evaluate farmer knowledge on PTM before the training session, participants were 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). Based on filled questionnaires, we built a "knowledge index" for each farmer, which corresponded to the percent of questions answered correctly.

We first held a 2-h workshop with the 13 participants to introduce fundamentals of biological invasions and pest management. Our aim was to show farmers that the invasion problem they face locally is a widespread phenomenon. We then focused on describing the biology of the pests, presenting key morphological characters to differentiate the three PTM species (*T. solanivora*, *P. operculella*, and *S. tangolias*). We then moved to a 1-h field session presenting procedures for PTM monitoring. Each farmer assembled three traps (one for each PTM species) using materials we provided them (Fig. 2a): dome-like plastic containers, pheromones specific for each PTM species (Pherobank, Wageningen, NL), and metallic threads. Farmers were also provided with one minimum–maximum thermometer (ERTCO,

Dubuque, IA) and a field book. Each farmer then went back to their community, fixed the traps on wooden sticks, and placed them in a potato field planted approximately 3 months earlier. Starting in October 2006, they recorded trap catches and temperatures every week for 8 weeks. Despite the lack of replicate sampling units in each community, it is likely that the extended time period and frequency of moth sampling allowed us to obtain a good estimation of the abundance of PTM in each locality. In each village, the 13 farmers also collectively evaluated damages (low, intermediate, and high) produced by PTM on potato tubers in stores by checking for holes made by young PTM larvae when burrowing into the tuber.

Fig. 2 Pictures of the participative monitoring performed with members of the Kichwa communities in the Simiatug valley. a Photograph showing 8 of the 13 participants with the material to perform the monitoring. Other people on the photograph are staff of the college and of the outreach project. b Community members checking adult moths identity with a stereomicroscope (left) and locating their own study site on a map of the region (right)

Third Session: Data Analysis

In December 2006, we met with the participants to compile and analyze their data. The approach used was largely that of learning-by-doing as local community teams and trainers

jointly recorded, compiled, summarized, graphed, and discussed field observations. As a first step, data compilation was divided into two practical sessions. Step one was to check the identification of each PTM individual collected in the traps using stereomicroscopes provided during the sessions (Fig. 2b). The second step was to locate precisely on a map of the region where they had performed their monitoring (Fig. 2b), allowing for the documentation of spatial dimension of the distribution of the pest and also of altitudes of the different villages.
Then, we discussed the potential factors that could explain differences in measured abundance of the three PTM species among villages. In order to make the analysis of the results easier, it was limited to three variables that both showed evident variations among the 13 communities and had been identified as key drivers of PTM abundance: air temperature, number of inhabitants, and remoteness of the village from Simiatug (other parameters; see Table 1). During their field work, farmers had registered air temperatures and provided an estimation of the number of inhabitants (variable "village size") in their communities. This parameter was likely to be a good indicator of the intensity of commercial exchanges between the village and Simiatug and could potentially be correlated with PTM densities in the valley. In order to measure the variable of "remoteness," we asked each farmer the travel time from Simiatug to their community. For each village i, rank of remoteness, R i , was then calculated by the normalized values of time, T i as follows:

$$R_i = \frac{T_i}{\sum_i^{13} T_i}.$$

The possible range of R i is from 0, the village Simiatug itself, to 1, the theoretical farthest community from Simiatug (see Table 1). The use of a normalized value of remoteness (see Eisenberg *et al.* 2006) allows potential comparison with other studies. Despite of its relatively small scale, our study area therefore encompassed a wide range of remoteness values, some villages being as close as half an hour from Simiatug and other distant to up to 5 h.

Farmers then schematically plotted on blackboards PTM densities against each of these three variables (air temperature, village size, and remoteness) to identify potential relationships. Data analysis was a hard step for farmers. We facilitated this process by drawing the graph and then asking each farmer to plot the value of PTM abundance and the corresponding factor (*e.g.*, temperature) recorded in the community of each farmer. In order to test the statistical significance of these graphical results, the authors further conducted

additional statistical analyses using general linear models (GLM) to probe the significance of results found by farmers. GLMs were used to test for effects on numbers of male moths captured of all measured variables at each site (altitude, temperature, remoteness, village size, potato variety, and rainfall). None of these factors were significantly correlated among each others (Spearman rank test, $R < 0.5$, $P > 0.23$) except 'altitude' and 'temperature' ($R = 0.96$, $P < 0.01$). We included the term 'site' in the GLM analysis to allow within-site comparisons while controlling for variation resulting from unmeasured site-specific parameters. The change in abundance of species due to each effect was modeled as an interaction term between this effect and the species factor. For example, the interaction between remoteness and species models how the abundance of species changed with remoteness. The more parsimonious model was identified using the Akaike's Information Criterion (AIC; see Venables and Ripley 2002). We used the likelihood ratio test (LRT) to test the difference between the initial model and the reduced model dropping an 'effect' term (Breen *et al.* 2007). All analyses were performed using the mass library for R (R Development Core Team 2006).

Fourth Session: Evaluation and Recommendations for PTM Management

The last session consisted of (1) the oral evaluation of the participatory monitoring by each participant and (2) recommendations for the integrated pest management (IPM) of PTM. Recommendations were based on the infestation levels and species identity the farmers had monitored under field and storage conditions in their community. These guidelines followed classical approaches from integrated pest management: cleaning store rooms, keeping the harvested potatoes covered and using a biopesticide (*e.g.*, *P. operculella* Granulovirus, PhopGV), exposing potato seed to the sun, hilling up of soil around plants or rotating crops (Pollet *et al.* 2004). In regions such as Simiatug where PTM densities are low, these simple recommendations are highly effective to control pest damages. However, in regions presenting high PTM densities, further IPM options such as participatory farmer field schools (see Pumisacho and Sherwood 2005) are necessary for an effective control of the pest. At the end of the session, we reevaluated participant knowledge on basic and practical PTM issues with the 20-item questionnaire used for the first session. We further assessed student learning by comparing their knowledge before and after the training session using a Wilcoxon Mann–Whitney test.

Results

Participation and Learning of the Community Members

Because of their vested interest in the research results and familiarity with the outdoors and work in the field, young community members were highly motivated and especially conscientious and reliable field workers. Field notes on trap catches and temperatures were generally rigorously reported in book notes that they provided us, and PTM species sorting was satisfying during the hands-on sessions (regarding identification checking). Organized meetings and informal discussion with community members were useful to create trust between partners. As a consequence, high levels of commitment to the monitoring and data analysis of PTM species were displayed by all community members. In talking with farmers at community meetings, they acknowledged that they were not aware of the risks caused by PTM before the participatory research (this was conformed by our questionnaire; see Fig. 3). Adult captures in pheromone traps revealed, however, the existence of infestation by PTM in the Simiatug valley, which was confirmed by the detection of larvae in potato storage surveys. Data from the questionnaires filled by farmers before and after participative sessions confirmed that participants significantly learned from it (two-sided Wilcoxon Mann–Whitney U test, $U \leq 1$, $P < 0.001$, $N = 13$ for both types of knowledge), especially in practical terms (Fig. 3).

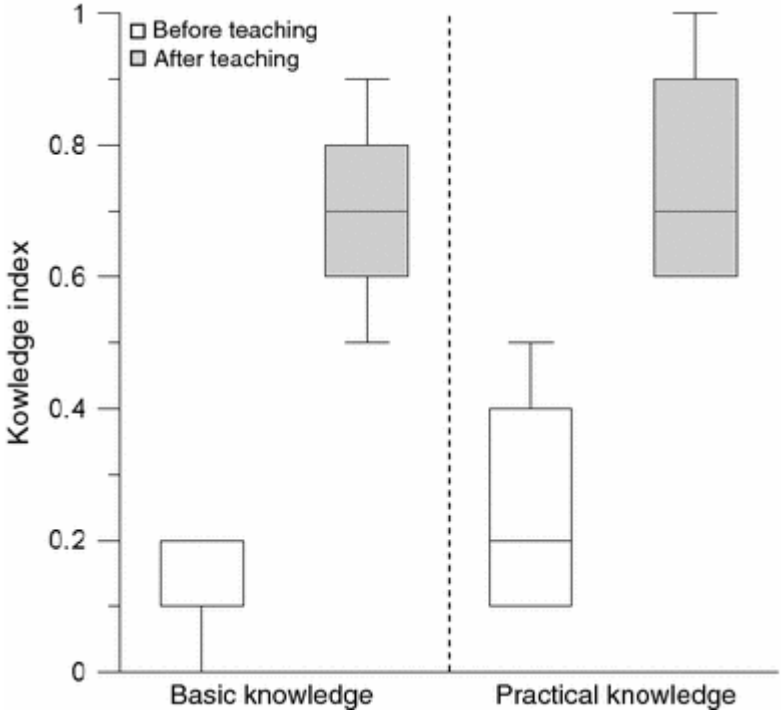

Fig. 3 Box-whisker plot of the basic and practical knowledge on tuber moth management of the local participants (N = 13) before and after sessions implemented in our community-based monitoring. The knowledge index was calculated based on a questionnaire including 20 items, 10 on basic issues (biology and ecology of the pest) and 10 on applied issues (pest management) (see "Methods" section). The three bars of the box consist of the median and the upper and lower quartiles in the distribution. The endpoints of both whiskers indicate minimum and maximum values

PTM Abundance in the Field

In general, the monitoring revealed low levels of catches of PTM species at all sites (<6 ind. day−1). The most abundant species in the Simiatug valley was *S. tangolias* (1.71 ± 1.6 ind. day−1, N = 13). *P. operculella* was rather abundant in three villages (1.16 ± 2.07 ind. day−1, N = 3) but had very low densities in the 10 others (0.11 ± 0.26 ind. day−1, N = 10). *T. solanivora* exhibited low density levels in all communities (0.72 ± 0.60 ind. day−1, N = 13). Farmers quickly pointed out the great variability in PTM densities among the different communities. In an attempt to explain this variability, participants investigated the influence of three variables, mean air temperature, village size, and village remoteness (see "Methods" section) that were markedly different among villages. Mean air temperature varied from 10.9 to 16.2°C, and village size ranged between 50 and 3000 inhabitants (Table 1). The least remote community has a remoteness value of 0.03, and the most remote village has a remoteness value of 0.23 (Table 1). Both air temperatures and village sizes were poorly correlated with PTM abundances (not shown). We found that the three PTM species were differently associated with remoteness of the 13 villages (Fig. 4a–c). *T. solanivora* showed a significant exponential decrease in abundance with an increase in remoteness from the closest to the farthest village to Simiatug (exponential, $R^2 = 0.62$, $P < 0.01$). In contrast, *S. tangolias* and *P. operculella* densities show no significant trend as a function of remoteness ($R^2 < 0.25$ and $P > 0.47$ for all models). Of the six factors included in the GLM analysis (see "Methods" section), only remoteness, species, and their interaction significantly affected the abundance of caught PTM adults (Table 2). Significant interactions with species indicated that the three PTM species responded differently to the remoteness from Simiatug.

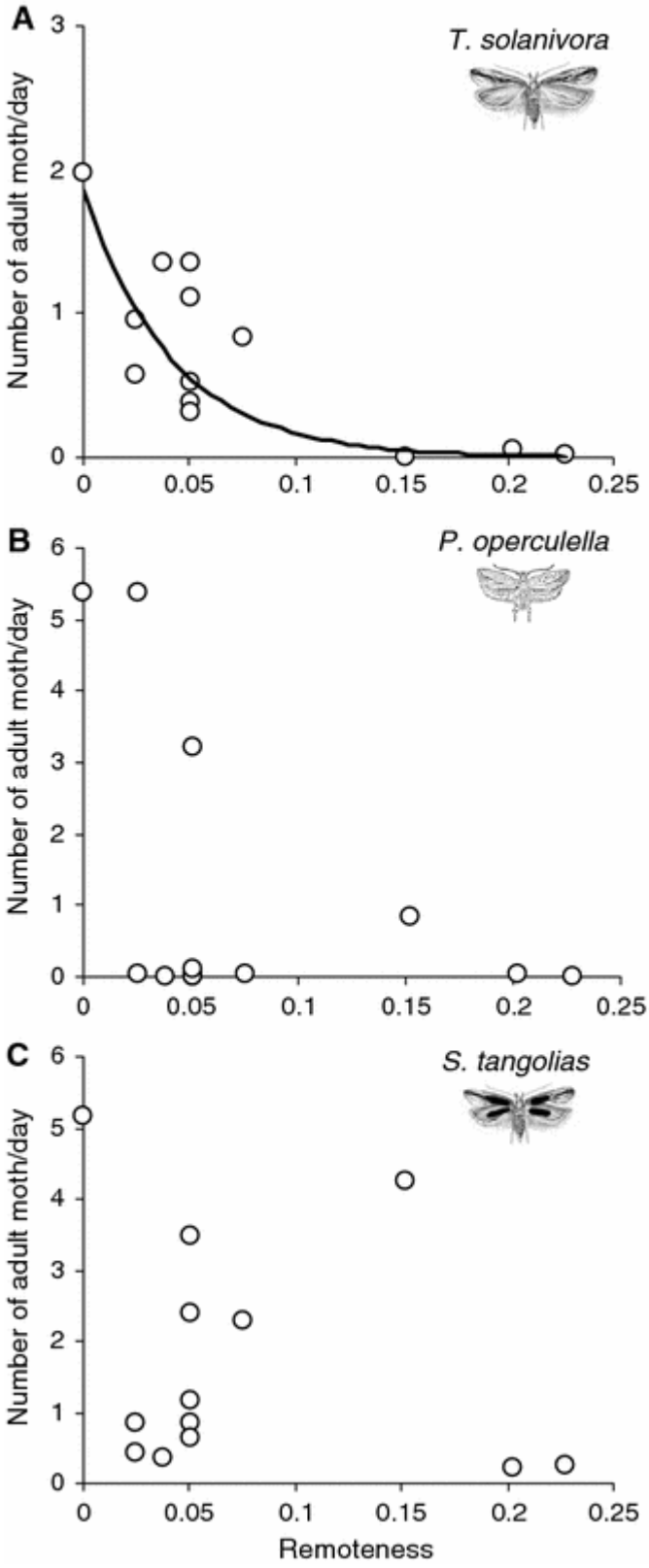

Fig. 4 Relationship between tuber moth densities and village remoteness from Simiatug. a *T. solanivora* (exponential fit, $R^2 = 0.62$, $P < 0.01$), b *P. operculella*, and c *S. tangolias* (non-significant relationships)

Table 2 Results of the generalized linear model's deviance analysis on PTM adult species catches in Simiatug

Effect	**Terms included in the initial model**	**AIC**	**Δ AIC**	**LRT**	***P* value**
Remoteness × species	All	230.4	8.4	7.32	0.005
Species	Remoteness, variety, species	227.3	3.3	5.45	0.016
Remoteness	Remoteness, variety, species	228.0	4.0	5.85	0.011

The significance of each of the eight factors initially selected (altitude, temperature, remoteness, village size, potato variety, rainfall, site, and species; see "Methods" section) was computed using model simplification and Likelihood ratio test (LRT). We started with a model including the effect of all factors plus their interaction and then removed higher-order non-significant terms until all remaining terms were significant. The table gives the contribution of these remaining factors that significantly explain changes in the abundance of PTM in the valley. AIC = Akaike's information criterion of the initial model after the removal of the 'effect' term. ΔAIC corresponds to the difference between the AIC of the initial model and that of the reduced model

Discussion

Research Findings

In view of worldwide reports of increases in agricultural pest invasions with the movement of goods and people, it has become ever more important to incorporate the dynamics of interactions between societies and (agro)ecosystems in studies on pest dispersal (Scheffer *et al.* 2002; Lockwood *et al.* 2007). In many cases, however, surveys are performed once the invasive pest species has become established, and the link between its distribution and human movements is hardly detectable at a local scale (With 2002). In this context, anthropogenic environmental changes such as road rehabilitation that cause populations to move and settle in new ways can provide the opportunity to observe the relationship between environmental changes and invasive species dispersal (see Eisenberg *et al.* 2006 for a similar example with the dispersal of human pathogens). In our study, the rehabilitation of the road between Guaranda and Simiatug had recently increased the exchanges between the two places (Culqui 2005) and is likely responsible for the relatively high PTM densities found in the

village of Simiatug, otherwise isolated by natural barriers. From this source population in Simiatug, *T. solanivora* showed significant trends in densities across a gradient of remoteness, even after adjusting for village size and temperature. Village size significantly affected PTM abundance in the Simiatug valley. Several factors are correlated with this variable, such as the area cultivated with potatoes or the presence of potato storages (tubers heaped under a basic shelter). In Ecuador, tuber infestation by PTM is habitually higher in potato storages than in the fields (Dangles *et al.* 2008). Storages indeed offer optimal conditions for PTM development, such as protection from coldest temperatures and against rainfall (Keasar *et al.* 2005). As the storages are located nearby the cultivated fields, part of the adult PTM population sampled in the traps probably undergoes its larval life cycle within storages. The significance of village size as a driving factor of PTM abundance may therefore be more related to the presence of storages than to the area of cultivated potatoes. Another important factor is that larger villages are more attractive to human flows and commercial exchanges than smaller ones (see Gilbert *et al.* 2004) and have therefore higher probabilities of being visited by people who transport infested potato seeds.

Our results indicated that villages farther from Simiatug had lower infestation rates by *T. solanivora* than villages closer to Simiatug. Why was this relationship observed only for *T. solanivora*? One reason maybe that in Ecuador, *T. solanivora* has been observed to develop only on tubers of S. tuberosum, whereas the two other species can grow on tubers, stems, or foliages of S. tuberosum, as well as on cultivated and wild Solanaceae (S. lycopersicum and S. nigriscens). The features of wide host plant spectra together with ample thermal tolerances (especially for *S. tangolias*) may increase the probability of a successful establishment in remote regions despite low dispersal rates. This could explain why *S. tangolias* was able to maintain populations in the more remote villages of the valley despite limited commercial contacts. Another interesting result of this study was that in contrast to a previous study in a high PTM invasion zone (Dangles *et al.* 2008), PTM species distribution was not related to air temperature. This suggests that mechanisms structuring invasive pest populations at the invasion front where PTM densities are low are different from those occurring in areas invaded for a longer period.

Obviously, these results are limited in space and time, and require further research and a greater range of results to permit a more robust analysis and validation. For example, additional analyses of insect population genetics could elucidate dispersal patterns across the landscape, and data on human migration patterns might provide information on causal linkages between remoteness and risks of the propagation of invasive species. In a similar

vein, looking at changes in incidence compared with changes in remoteness over time may provide additional causal information about how road development affects invasive pest dispersal, because the time scale of these social changes may take years or decades (Eisenberg *et al.* 2006). The remoteness and large number of possible sampling sites in populated rural areas such as the Andes demands that scientists develop collaborations with local communities to carry out such studies in a timely and rigorous way. Standardized, repeated, quantitative measures would be a useful way of determining the correlates of invasion success. It would also shed light both on attributes of species that make them likely to invade and have negative impacts, and on characteristics of the recipient environments that make them resistant or vulnerable to invasion. In turn, remote communities may be able to benefit from the more mechanistic pest management knowledge brought in by outside professionals to face emerging infestations by pests such as PTM. Monitoring would help these communities with the early detection of emergent invasions, within the window of opportunity where eradication efforts may be successful.

Practical Applications for the Communities

A participatory monitoring system of natural resources and associated threats is expected to be successful only if the local participants directly benefit from their involvement (Stuart-Hill *et al.* 2005). Several studies have reported the difficulties of involving local communities in resource management issues (see Borgerhoff Mulder and Coppolillo 2005; Williams 2007). Our experience in Simiatug was that farmers involved in the monitoring displayed a high level of commitment to the pest monitoring program although there are still challenges to reaching people in surrounding communities. Three main reasons may explain this result. First, and most importantly, community members were conscious of their dependence on their natural resources. Because they derive nutritional, financial, and even cultural benefits from harvesting potatoes (see Brush 2004), farmers were willing to contribute to any action for protecting that resource. Second, all of the participating farmers were also students in an adult high school program in Agriculture in the main town of Simiatug, thus they were more open to performing monitoring activities in their own communities than perhaps a non-student farmer would be. Third, the monitoring program we developed was simple, required a minimum of training and education, and was supported by local educational authorities. It also required little equipment, time, and financial resources, and had a short process time from data to management actions on-the-ground.

Both oral and written evaluations of the participative sessions revealed that farmers will be able to better manage their resources, after the participatory research implementation because they realized, from their own work, the spatial distribution of the pests in the valley and some potential mechanisms of their dispersal via the road network. A major benefit of our community-based research is therefore that future management interventions can be designed as a direct response to the results of monitoring activities and analyses of collected data, rather than just being based on perceptions of the PTM threat. More importantly, we think that the data on tuber moth trapping clearly enhanced local awareness about the need to control the pests before they became too numerous. The main specific management action taken by farmers was the systematic checking for PTM when buying potato tubers in the Simiatug market before transportation to their community. We also stressed the point with our local partners that benefits of the monitoring to the communities may also be over the longer term, in the form of a reduced probability of production collapse through PTM infestation. Unfortunately, we have no data about the transfer of knowledge from the participants to other community members in the valley of Simiatug. However, our group has evidence that each participant from farmer field schools similar to that we presented in this article can spread their knowledge to at least five people of their community (Villares 2008).

Participants and high school authorities expressed their interest of continuing with pest monitoring in the Simiatug region in the future. This monitoring program is currently continuing in the Simiatug valley and has been successfully extended to 42 participants in 2009. It provides farmers with information that allows them to predict more effectively potential threats to their crops and to quantitatively assess trends in agricultural landscape changes and the effects of pest control strategies. However, ensuring the sustainability of locally based monitoring systems, even when they have been designed to require minimal resources and to be reliant on locally available expertise and materials, is not an easy task. It will depend on the degree to which the participatory monitoring can increase the benefits to local farmers as a function of the cost incurred by monitoring. It will also depend on the extent to which farmers would spread their knowledge to other members of the community, an issue that we are currently studying through questionnaires and agent-based models. Further quantitative simulations of the net present value of potato harvests (the present value of the expected future revenues minus the present value of the expected future costs) with and without monitoring would also be useful to measure the benefit of following the monitoring on the long term (see Hockley *et al.* 2005).

Perspectives and Potential of Generalization

Monitoring is a fundamental part of environmental science, and long-term data are particularly crucial for documenting and predicting the spread of exotic pest species (Lovett *et al.* 2007). Community-based investigations in the context of invasive agricultural pest management can be a promising approach, especially in developing countries that often face limited funding and administrative capabilities. The experience from Simiatug is that collecting monitoring data using traps was a useful approach that can lead to better informed management interventions for controlling invasive pests, especially in remote invasion fronts. Given that these agricultural pests are essentially related to trade and human mobility, it would be essential to scale up a participatory monitoring approach similar to that we presented in order to improve regional cooperation to manage and reduce risks related to PTM. We are currently extending our community-based monitoring into other parts of Ecuador, with successful results in several communities of the Chimborazo and Bolívar Provinces. At a larger scale, it would be critical for developing nations of the Northern Andes and elsewhere in the world to invest in and cooperate toward building better understanding and capacity to deal with invasive agricultural pests (see Galindo-Leal 2001). Although the Andean countries have recognized the problems associated with invasive pest species for several years (see Ojasti 2001), a comprehensive approach to this issue still has to be developed. Establishing partnerships between national institutions will undoubtedly be a key issue in developing participatory research in the context of invasive pest management. In the present study, the establishment of a collaboration between research (Pontifical Catholic University of Ecuador, PUCE), technical (National Agronomy Institute of Ecuador, INIAP), and educational institutions (College of Agriculture of Simiatug) at both national and local levels revealed an effective strategy to empower local lay science. We believe that the implication of an international organism (Institute for Research and Development, IRD) and a foundation (McKnight Foundation) being involved in the project have also helped in supporting innovation to overcome the practices of local institutions that sometimes inhibit the interactive approach to science advocated above. It is likely that doing science separately at the local level would never produce the valuable outcomes presented in this study (see Fortmann 2008).

Conclusion

In this study, scientists would have hardly been able to study the dynamics of invasive population on a weekly basis in such remote invasion fronts without the help of local farmers

(the whole tour through the 13 communities, many of which are only accessible by walking, required about 5 days). Reciprocally, farmers would not have been able to detect risks associated with PTM without scientists. As material and human means for ecological monitoring in developing countries are scarce there is a huge need for innovative solutions. Including local people in these activities is not just an opportunity to increase the effectiveness of early detection of invasive species but also a powerful education tool for growing awareness on the magnitude of the challenge they pose.

Acknowledgments

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3.2. Modélisation multi-agents de la dispersion induite par l'homme d'espèces envahissantes dans le paysage agricole

Résumé en français

Les modèles à base d'agents (ABM) sont des outils privilégiés pour intégrer la complexité de l'invasion d'un ravageur au sein de systèmes socio-écologiques agricoles, et cependant, on ne retrouve dans la littérature que très peu d'exemples d'utilisation dans un tel contexte. Dans cette étude, il a été développé un ABM qui simule les interactions entre des agriculteurs et un insecte envahissant ravageur des cultures dans un paysage agricole des Andes tropicales. Les objectifs de celle-ci étaient d'utiliser le modèle 1) pour évaluer l'importance des déplacements des agriculteurs et leur connaissance en terme de contrôle sur sa dispersion et 2) pour l'utiliser comme un outil éducatif afin de former des communautés d'agriculteurs confrontés à ce ravageur. Le modèle combine un sous-modèle écologique, simulant la dynamique spatio-temporelle des populations de ravageur (automate cellulaire incluant les facteurs exogène du paysage), avec un sous-modèle social dans lequel a été incorporé des agents (agriculteurs) transportant potentiellement le ravageur de par leurs déplacements de villages à villages. Les résultats des simulations ont révélé que les déplacements des agents et la connaissance du ravageur avaient un effet significatif non-linéaire sur la dynamique d'invasion du ravageur, confirmant les études existantes sur l'expansion de maladies par des épidémiologistes. Cependant, l'hétérogénéité des connaissances du ravageur au sein d'une communauté d'agents s'avèrerait n'avoir qu'un faible impact sur la dynamique d'invasion (hors valeurs extrêmes). Les évaluations des sessions de formation utilisant un ABM suggèrent que les agriculteurs seraient mieux à même à gérer leurs récoltes suite aux formations dispensées. De plus, en démontrant aux agriculteurs que les ravageurs ne se dispersaient pas uniquement en fonction de décisions individuelles, mais surtout en fonction des interactions multiples et répétées entre individus au fil du temps, le modèle a permis d'introduire une réflexion et des questionnements relatifs aux réseaux sociaux et à la psychologie des individus, questions habituellement négligées dans les programmes de protection intégrée des cultures contre les ravageurs.

Agent-Based Modeling of Human-Induced Spread of Invasive Species in Agricultural Landscapes: Insights from the Potato Moth in Ecuador

François Rebaudo, Verónica Crespo-Pérez, Jean-François Silvain and Olivier Dangles (2011)

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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: 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 2005a) 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 (Liebold 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.*Gong 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 ran 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 to 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.

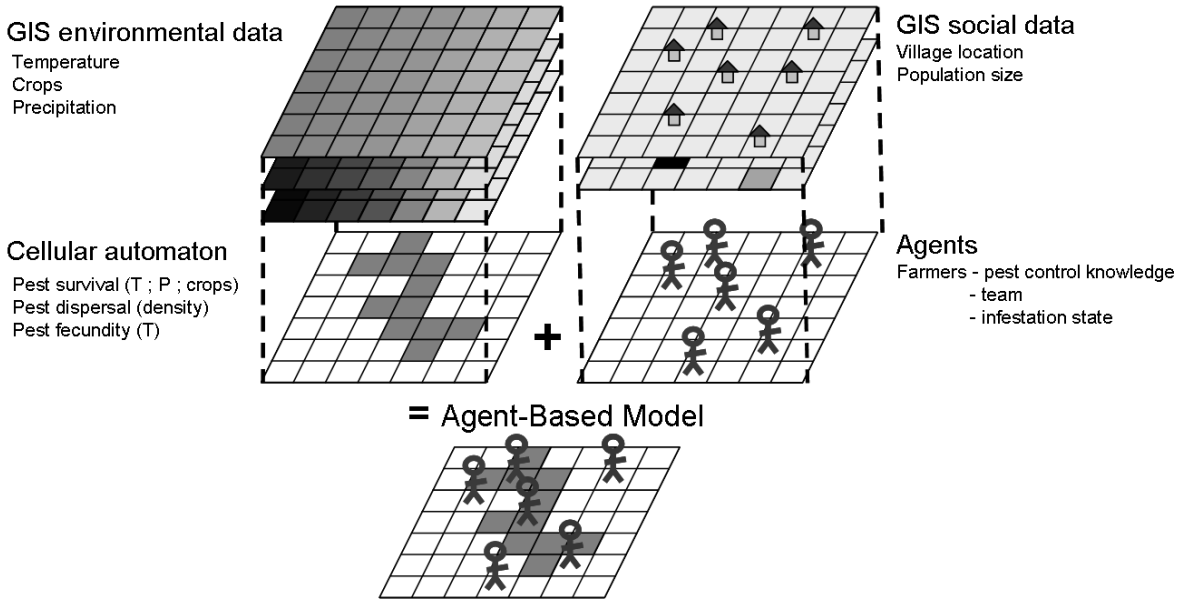

Figure 1. Schematic representation of the model structure

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 and is detailed in 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 × 20 km within the remote valley of Simiatug in the Central Ecuadorian Andes (see section 5) 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 moves 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 moves to an infested village (buying infested potato seed sacks), depending on his pest control knowledge (higher pest control knowledge leads to lower probability of buying infested sacks).

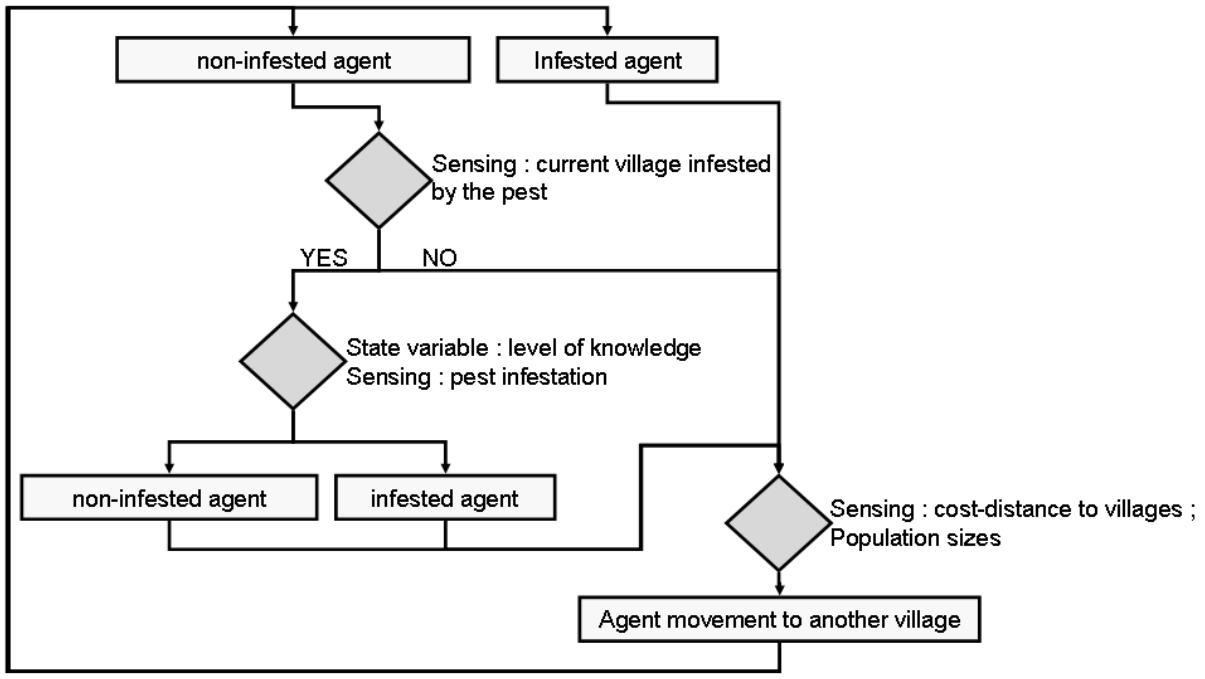

Figure 2. Agents' processes loop showing how farmers influence pest infestation spread. This loop is executed various times depending on farmers' traveling decisions during each timeframe.

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.

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). We are aware that the spatial configuration of our social landscape (see the frequency of infested farmer movements in Figure 4) likely influenced our results. Further studies including randomly generated social landscapes could help to quantify this effect on agents' movements and subsequent pest infestation dynamics.

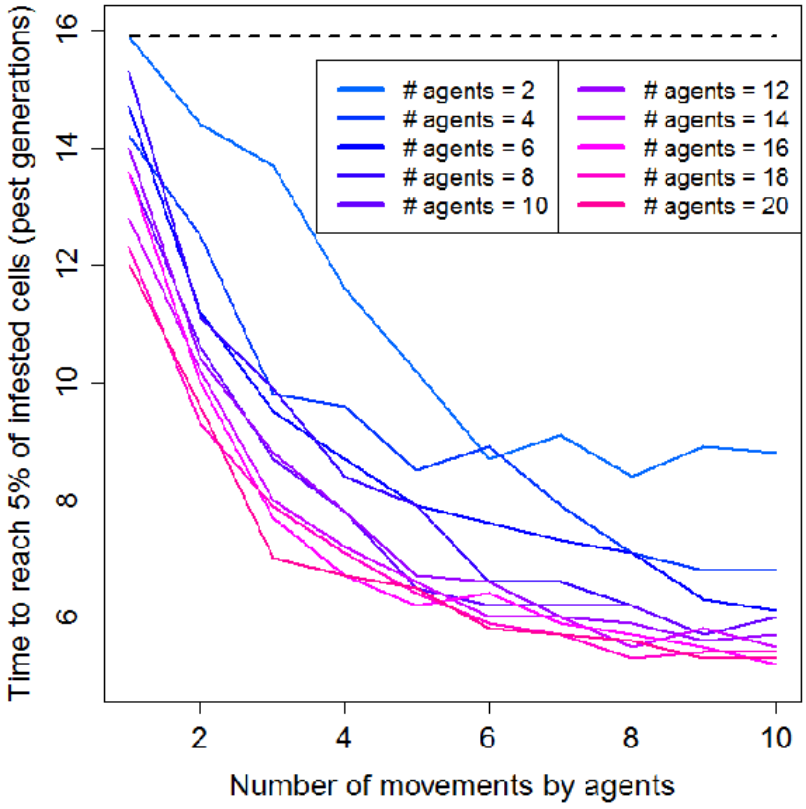

Figure 3. Influence of agents' movements (per pest generation) on pest infestation dynamics for different agent densities (n=2 to 20). The dashed line represents time needed to reach 5% of infested cells without agents (purely "biological" spread).

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.* Gong 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.

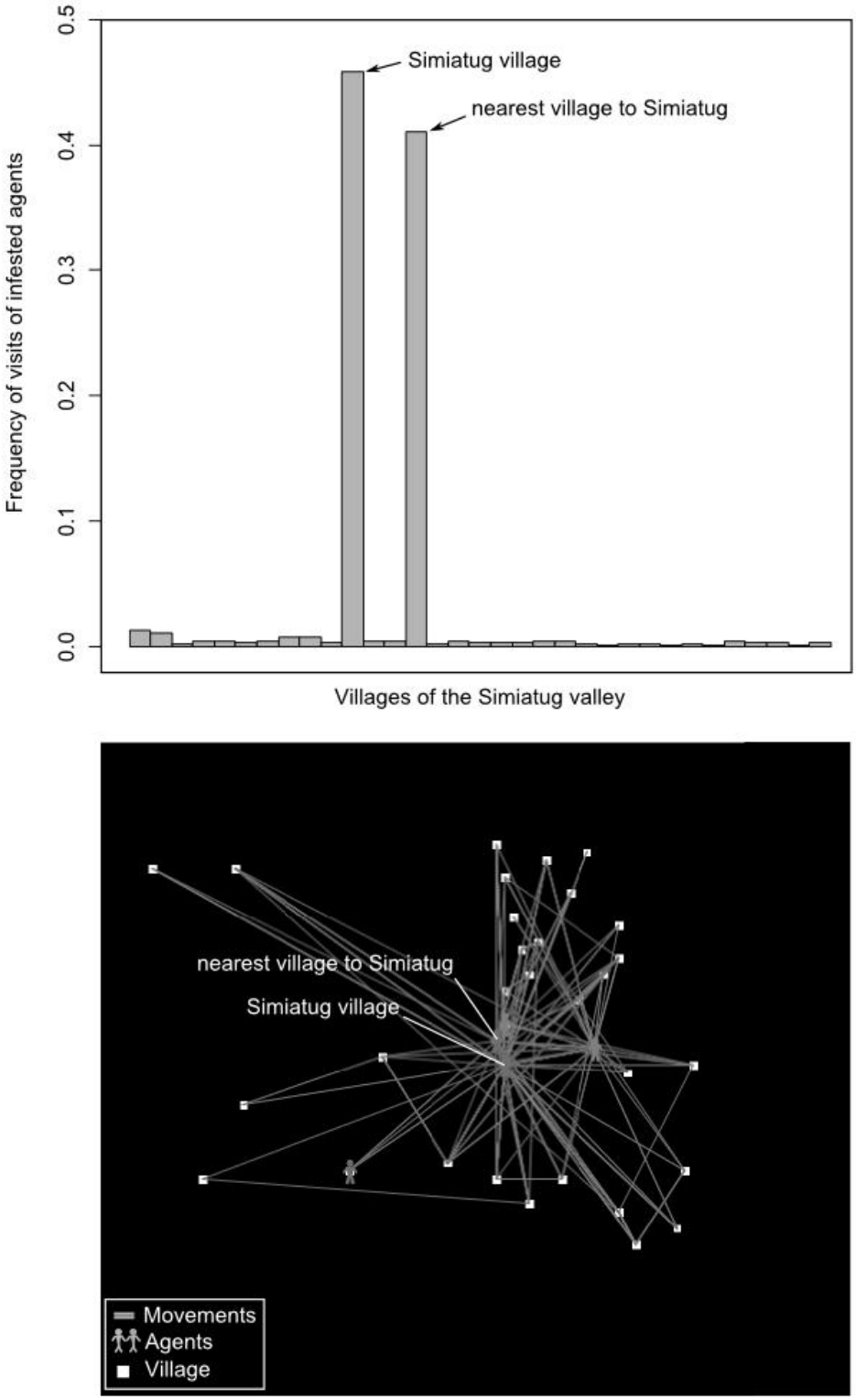

Figure 4. Frequency of visits of infested agents for each village and map of the Simiatug valley with agents' movements and villages location.

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 2). 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.

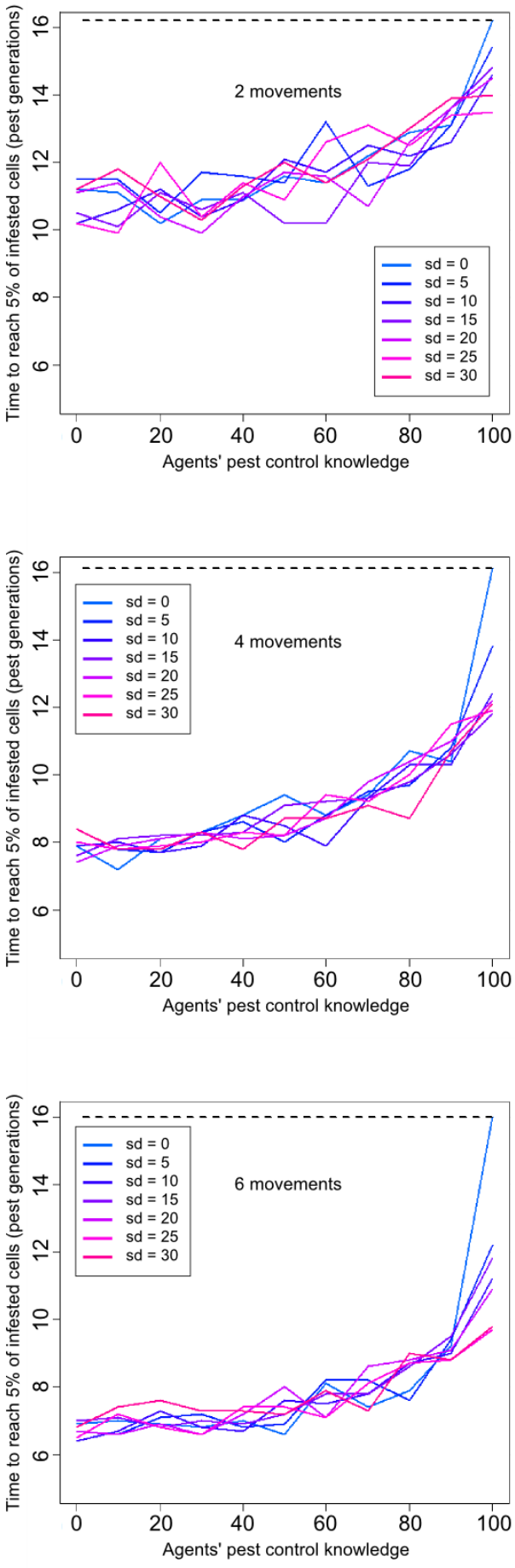

Figure 5. Influence of agents' pest control knowledge (means) and heterogeneity (standard deviation = 0 to 30%) on pest infestation dynamics for three frequencies of movements (2, 4, and 6). The dashed line represents time needed to reach 5% of infested cells without agents (purely "biological" spread).

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 and the absence of spatial clusters 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).

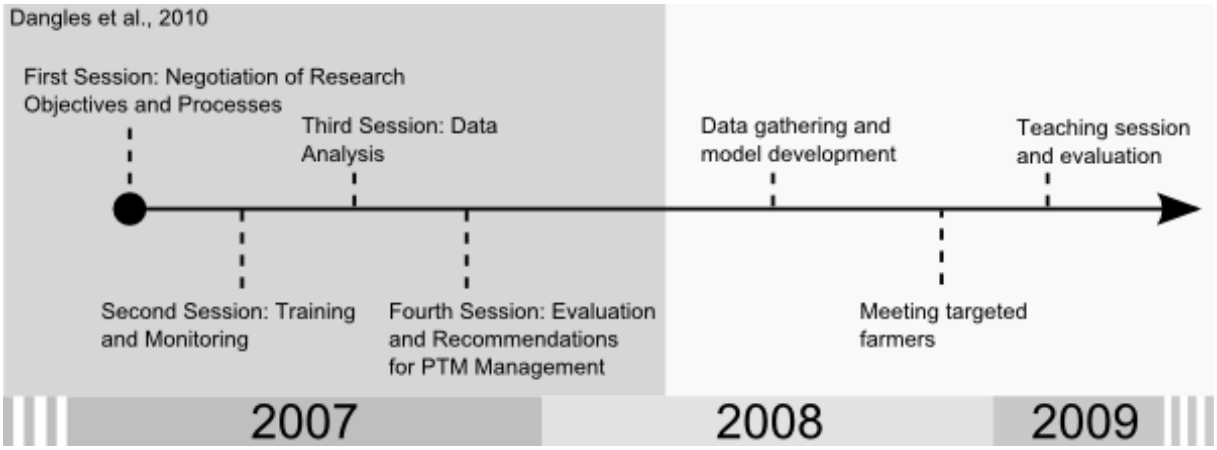

Figure 6. Timeline of the groundwork prior to the teaching session

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).

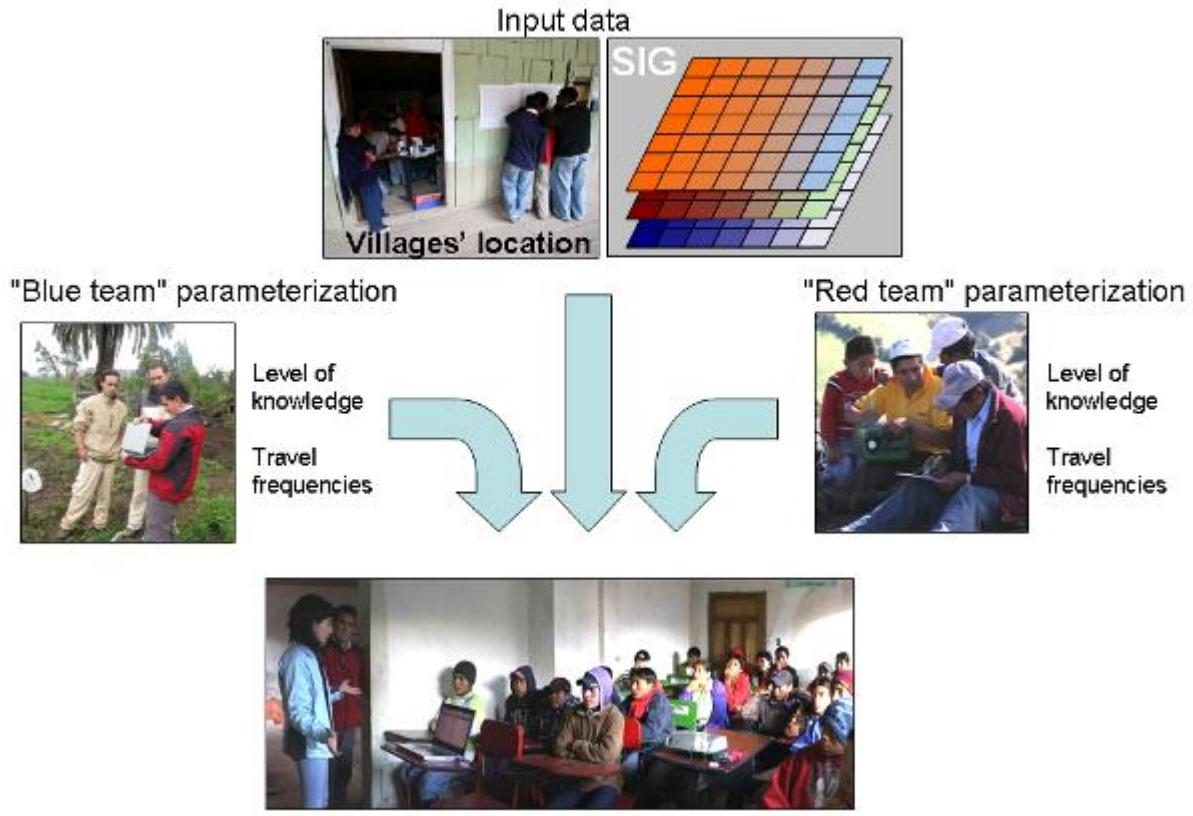

Figure 7. Teaching with an agent-based model in an agricultural valley of Ecuador

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 from the gaming session (initial)	Parameters values from the gaming session (final)
Parameterization		
Number of farmers	10	10
Number of movements per timeframe	6	3

Pest control knowledge	~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 Web sites 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.

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DISCUSSION GENERALE

Discussion générale

A travers l'exemple d'un complexe d'espèces de teignes de la pomme de terre dans les Andes équatoriennes, l'objectif principal de ce travail de thèse était de contribuer à une meilleure compréhension de la dynamique spatio-temporelle d'insectes ravageurs des cultures dans les systèmes socio-écologiques. Pour ce faire, il était nécessaire de développer des modèles visant à une meilleure intégration des activités humaines et de leurs conséquences sur les systèmes étudiés. Dans une première partie, cette discussion se propose de revenir sur les types de modèle développés dans ce travail et les choix dans la représentation des entités modélisées. La deuxième partie discute quant à elle la démarche de modélisation à travers des éléments de bonnes pratiques de modélisation. Enfin, une troisième partie présente les perspectives de recherches issues de ce travail de thèse.

1. Types de modèle et niveaux d'abstraction

Pour représenter les systèmes socio-écologiques, les modèles de ce manuscrit, implémentés via les plateformes de modélisation CORMAS (Bousquet *et al.* 1998) et NetLogo (Wilensky 1999), ont été construits via des types de modèle variés (automates cellulaires, individu-centrés et agent-centrés), à différentes échelles, et en considérant les insectes ravageurs au niveau de l'individu ou de la population (voir Table 1).

Table 1 : Caractéristiques générales des modèles développés (classés par chapitre, suivis d'un identifiant utilisé dans la suite de ce manuscrit : M1 à M5).

	Chapitre 1		Chapitre 2		Chapitre 3
	M1	M2	M3	M4	M5
Automate Cellulaire	- Populations d'insectes - Paysage fixe - Facteurs humains	- Paysage modifié par l'homme	- Populations d'insectes - Paysage fixe	- Populations d'insectes - Paysage fixe	- Populations d'insectes - Paysage fixe
Individu-centré	-	- Insectes	-	-	-
Agent-centré	-	-	- Groupes d'agriculteurs	- Groupes d'agriculteurs	- Groupes d'agriculteurs
Plateforme	CORMAS	NetLogo	NetLogo	CORMAS	NetLogo
Echelle[10]	20 x 20 km	générique	générique	3 x 3 km	40 x 40 km
Résolution[11]	500 m	générique	générique	500 m	500 m

Le choix du niveau d'abstraction (défini à travers les choix de l'échelle, de la résolution et du niveau d'organisation) est déterminant pour représenter les patrons spatio-temporels

[10] L'échelle représente la taille du paysage prise en compte dans le modèle (*e.g.* longueur × largeur dans le cas d'un paysage rectangulaire, comme c'est le cas ici).
[11] La résolution représente l'unité de base du modèle (équivalent au pixel dans le cas d'une image).

observables à différents niveaux (Grimm *et al.* 2005). A titre d'exemple, par la comparaison de trois échelles spatiales dans un contexte de biologie de la conservation (diversité des espèces de papillons finlandais à l'échelle locale, régionale et nationale), Cabeza *et al.* 2010 montrent que plus la résolution du système est faible, plus les entités à considérer seront nombreuses et les modèles complexes. Dans ce manuscrit de thèse, si les échelles sont différentes, en revanche les résolutions des modèles spécifiques au modèle d'étude des teignes de la pomme de terre sont similaires (Table 1, modèles *M1*, *M4* et *M5*). Ce choix, comme indiqué dans les articles correspondants, est un compromis entre les données du paysage disponibles (résolution de 1 km) et les capacités de dispersion du ravageur (environ 250 m). Puisque les questions qui ont conduit à ces modèles sont centrées sur la dynamique spatio-temporelle de ces insectes, il peut sembler intuitif que le choix des résolutions se fasse sur la base de leur capacité à se déplacer dans le paysage[12]. En tout état de cause, le choix approprié du niveau d'abstraction demeure un challenge dans ce type de modélisation car les processus écologiques et sociaux s'opèrent souvent à des niveaux d'abstraction différents (Chapin *et al.* 2009). A titre d'exemple, les évènements de dispersion d'insectes à longue distance induits par l'homme (« *long distance dispersal* », voir chapitre 1), ne sont pertinents qu'à l'échelle où ils s'opèrent (de village à village), et donc à une résolution permettant la représentation des villages. La détermination des résolutions auxquelles les effets des ravageurs des cultures s'opèrent est donc critique afin d'établir la stratégie de protection des cultures la plus pertinente pour l'agriculteur (voir Carrière 2011). Si les analyses de sensibilité se révèlent efficaces pour étudier l'effet d'une variable sur les sorties du modèle considéré (Oakley et O'Hagan 2004), les méthodes permettant d'étudier les effets du choix du niveau d'abstraction dans des modèles tels que ceux construits dans ce travail, restent à développer (Janssen et Ostrom 2006, Crooks *et al.* 2008), principalement parce que les processus représentés sont implémentés pour un niveau d'abstraction donné[13].

2. Bonnes pratiques de modélisation

Le besoin d'établir de bonnes pratiques de modélisation n'est pas nouveau (Scholten 1999). Dans leur révision de la littérature sur les modèles écologiques (dans un contexte de prise de décision environnementale), Schmolke *et al.* 2010 identifient les facteurs expliquant que de telles pratiques ne soient pas unanimement établies et remettent à l'ordre du jour la

[12] Même si Cabeza *et al.* 2010 rapportent que « *the choice of the planning unit and planning method is often driven by the availability of data rather than by how appropriate the methods are.* »

[13] A titre d'exemple, concernant les changements de niveaux d'organisation, Crooks *et al.* 2008 soulignent que « *as we aggregate, we can unwittingly change the kinds of processes that agents enable, the kinds of mobility intrinsic to their location, and the scale at which they exist.* »

notion de bonnes pratiques de modélisation, comme protocole de référence pour la formulation, la documentation, le contrôle, les analyses et les applications des modèles. Cette partie discute des notions clés de vérification et de validation des modèles, puis de la reproductibilité des résultats, qui relèvent d'une documentation adéquate associée aux modèles.

2.1 Vérification et validation des modèles

Utilisées dans leur sens premier, la vérification et la validation des modèles numériques des systèmes naturels seraient impossibles[14] (voir l'article de référence de Oreskes *et al.* 1994). En effet, du latin *verificare* (présenter comme véridique), la vérification représente "l'action de s'assurer de l'exactitude de quelque chose" (ici un modèle), par la démonstration, ce qui n'est possible que dans le cas d'un système clos. La validation, du latin *validare* (déclarer valide), représente quant à elle "l'établissement d'une légitimité", supposant une cohérence interne et l'absence d'erreurs détectables, difficilement applicable, voir trompeur, dans le cas des résultats d'un modèle. Les modèles numériques développés doivent cependant: i) être implémentés de manière à correspondre au modèle conceptuel, et de la sorte reproduire les observations utilisées pour le paramétrage (*i.e.* vérification) et ii) pouvoir reproduire des patrons et observations non utilisées dans le développement mais qui s'avèrent valides (*i.e.* validation) (voir « *Pattern-Oriented Modeling* », Grimm *et al.* 2005, et Parker *et al.* 2003[15]). Les modèles développés dans ce manuscrit contribuent à la généralisation de bonnes pratiques de modélisation en intégrant dans les articles correspondants, les éléments de vérification et de validation considérés (tels que définis dans ce manuscrit, et que le lecteur pourra retrouver dans les annexes des articles). De par la démarche ascendante adoptée (automates cellulaires, modèles individu/agent-centrés), les modèles conceptuels et leurs implémentations apparaissent comme plus réalistes (Grimm 1999) que ceux issus des approches descendantes, et ce qui laisserait supposer une validation plus aisée. Cependant, la validation des représentations de systèmes socio-écologiques demeure un point faible des approches ascendantes, identifié il y a près de dix ans (Parker *et al.* 2003), et qui reste toujours d'actualité (An 2011). Ce constat est notamment pertinent pour les processus de prise de décisions des agents (en tant qu'entités des modèles), représentant des comportements humains.

[14] « *Verification and validation of numerical models of natural systems is impossible* » Oreskes *et al.* 1994
[15] « *verification means building the system right, and validation means building the right system.* » Parker *et al.* 2003

2.2 Reproductibilité des résultats

La reproductibilité (*i.e.* la confirmation des résultats et conclusions d'une étude obtenue de manière indépendante à cette étude) est considérée comme un standard scientifique de premier ordre (Jasny *et al.* 2011). Cependant, dans les sciences de l'informatique et de la simulation numérique, la reproductibilité (et donc l'évaluation des résultats) atteint des limites de par la nature des travaux réalisés (*e.g.* le volume des données et leur analyse *via* différents logiciels[16], voir Peng 2011). Dans ce contexte, Peng (2011) suggère que les données et le code ayant servi à leur interprétation, soient accessibles en complément des articles scientifiques (voir Fig. 1 qui représente les différents niveaux de reproductibilité).

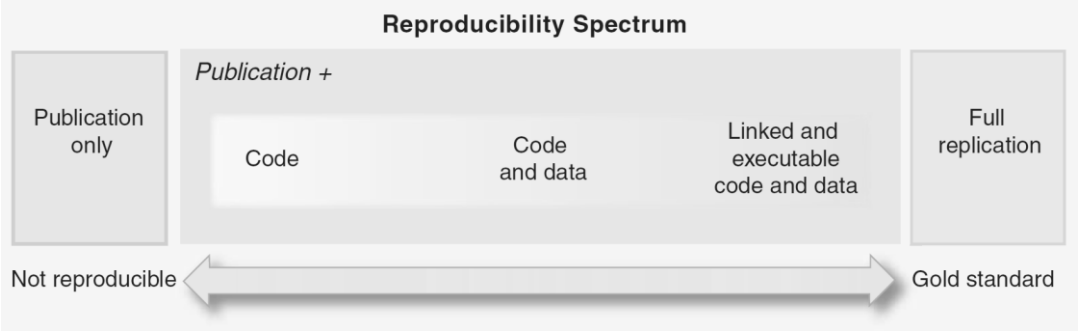

Fig 1. : Standards de reproductibilité, depuis la disponibilité du simple article jusqu'à la mise à disposition du code lié aux données correspondantes (d'après Peng 2011).

Dans ce manuscrit, tous les codes des modèles développés sont librement accessibles en annexes, ainsi que la plupart des données utilisées (incluses dans le code). La reproductibilité des résultats obtenus reste cependant limitée aux possibilités offertes par les revues scientifiques (*e.g.* format des annexes, voir Peng 2011). Elle n'est par ailleurs possible que lorsque les articles sont accompagnés d'une description complète du modèle et des théories associées, à l'aide de standards de description. Dans ce manuscrit de thèse, c'est le protocole « *Overview Design concepts and Details* » (ODD, voir Grimm *et al.* 2006, Grimm 2010) qui a été utilisé à cette fin. Contrairement au langage de modélisation UML (*Unified Modeling Language, e.g.* Berardi *et al.* 2005) plus largement répandu, le protocole ODD a été mis au point dans l'objectif de rendre les modèles agent/individu-centrés (et automates cellulaires) moins sujets à la critique de non-reproductibilité. Le fait qu'une étude soit reproductible ne garantit pas pour autant sa qualité (Peng 2011), mais la reproduction d'un modèle contribue à rendre l'évaluation de sa vérification et de sa validation plus aisée (Wilensky et Rand 2007).

[16] « *Interactive software systems often used for exploratory data analysis typically do not keep track of users' actions in any concrete form.* » Peng 2011

Remettre à l'ordre du jour la notion de reproductibilité puis la rendre systématique contribuerait ainsi à renforcer la valeur scientifique des articles de recherche (*e.g.* les initiatives du journal *Biostatistics*[17] pour l'évaluation de la reproductibilité des résultats, ou le *Volterra Replication Prize*[18] qui récompense chaque année une étude reproduisant les résultats d'un article basé sur un modèle multi-agents). Au-delà des modèles présentés dans ce manuscrit, il semble que ce soit aux revues scientifiques d'exiger ce standard, mais aussi d'apporter des solutions plurielles pour la soumission du code et des données associées.

3. Perspectives de recherche issues de ce travail de thèse

3.1. Vers une meilleure compréhension des systèmes socio-écologiques

- ***Considérer la dynamique de communautés d'insectes***

Dans le premier chapitre (modéliser la dispersion d'espèces envahissantes dans un paysage hétérogène), la dynamique spatio-temporelle de populations d'insectes a été modélisée tout en intégrant des aspects relatifs aux actions de l'homme (infrastructures, déplacements et usage du sol, Table 1, *M1*). Si ce modèle explique la répartition spatio-temporelle d'une espèce de ravageurs, il n'intègre pas les interactions potentielles avec d'autres ravageurs, compétiteurs ou facilitateurs (voir Dangles *et al.* 2009). Cette intégration pourrait se révéler d'autant plus importante à d'autres niveaux d'abstraction, comme dans le cas du modèle *M2*, pour lequel le niveau d'organisation est celui de l'insecte (voir Table 1). Modéliser les interactions inter-specifiques reste par ailleurs un challenge majeur pour mieux comprendre la dynamique des insectes phytophages face aux changements globaux (voir Kaplan & Denno 2007), et dans ce contexte, les modèles de type individus-centrés constituent des outils de premier choix, bien que sous-utilisés.

- ***Intégrer et analyser l'hétérogénéité temporelle du paysage***

Dans ce dernier modèle (*M2*), le paysage est représenté de façon explicite (comme dans tous les modèles de ce manuscrit) afin d'intégrer l'hétérogénéité spatiale du paysage. Il est aussi hétérogène dans le temps (module de gestion de l'usage du sol). Dans le cadre de l'article associé (voir chapitre 1), cette hétérogénéité temporelle n'a cependant pas été analysée par la simulation. Rocca et Greco (2011), dans leur étude sur la biodiversité des insectes associés à une culture introduite, rapportent néanmoins des différences significatives d'abondance des espèces d'insectes en fonction des changements du paysage. Dans le cas du complexe d'espèces de teignes de la pomme de terre et des modèles associés (*M1*, *M4* et *M5*),

[17] http://biostatistics.oxfordjournals.org/content/10/3/405.full
[18] http://www.volterra.co.uk/custompage/replication-prize.php

et dans un contexte de changements globaux (*e.g.* simplification des paysage agricoles dans les Andes, voir Poveda *et al.* 2012 ; avancées des frontières agricoles en altitude, voir Stadel 2005), l'intégration de telles modifications dans le temps pourrait contribuer à une meilleure compréhension des systèmes étudiés et ainsi à l'exploration de scénarios prospectifs plus fiables.

- ***Approfondir la caractérisation des comportements des agriculteurs***

Le deuxième chapitre (approches pluridisciplinaires et couplage de modèles), contribue au couplage de modèles de sciences sociales avec les modèles d'écologie précédemment décrits. Plus particulièrement, il s'intéresse à la diffusion d'une innovation au sein d'une communauté d'agriculteurs. Bien que des approches similaires aient été étudiées (*e.g.* Berger 2001, Feola et Binder 2010), l'apport novateur de ce manuscrit est l'étude de leurs impacts sur la dynamique spatio-temporelle d'insectes ravageurs des cultures. Néanmoins, que l'approche soit théorique (*M3*), ou plus appliquée (*M4*), la caractérisation des comportements des agriculteurs reste exploratoire (voir Smajgl *et al.* 2011). Si des lignes directrices ont pu être établies (et extrapolées prudemment sous forme de recommandations pour l'évaluation de stratégies de lutte), l'intégration de comportements plus hétérogènes (*e.g.* agriculteurs profitant des innovations sans les transmettre, dilution de la qualité des formations), tout comme le développement d'aspects socio-économiques (voir Carrasco *et al.* 2012), permettraient d'affiner les scénarios établis, tout en réduisant néanmoins leur généricité. La question se pose alors de savoir si chaque système socio-écologique est spécifique ou alors si des tendances générales peuvent en être extraites. Comme vu précédemment, tout dépendra de la question scientifique à l'origine de la modélisation[19]. Des alternatives méthodologiques de représentation, comme les processus de conception innovante, tels que ceux en cours de développement dans le cadre de la gestion des services écosystémiques[20], seraient susceptibles d'apporter des éléments nouveaux. En tout état de cause et compte tenu de la difficulté à caractériser les comportements des acteurs (Smajgl *et al.* 2011), ces perspectives ne seraient envisageables sans une collaboration plus étroite avec des scientifiques en sciences humaines et sociales.

3.2. Des modèles comme outils de formation

Suite à une activité de recherche participative, une première approche de formation basée sur un modèle a permis de renforcer le passage des actions de recherche à celles de

[19] « *Modeling has to start with specific questions* », Grimm *et al.* 2005
[20] voir les travaux de l'UMR SADAPT

développement (voir chapitre 3). Bien que les agriculteurs n'aient pas participé au développement du modèle (voir les travaux de Voinov et Bousquet 2010 sur la modélisation participative), les retours positifs des agriculteurs ont conduit au développement d'un deuxième modèle de formation (voir Carpio *et al.* 2011). Ce dernier, développé spécifiquement pour être utilisé par les acteurs, repose sur un jeu où chaque participant prend le rôle d'un agriculteur dont les pratiques vont influencer la dynamique spatio-temporelle d'un ravageur des cultures sur ses parcelles et celles de ses voisins. Chaque participant a aussi la possibilité de partager ses compétences en termes de protection des cultures et ainsi de contribuer à une gestion du ravageur à l'échelle du paysage (jeu de rôle, voir Sciences au Sud n°59). Il a été testé avec succès dans une communauté des Andes équatoriennes, puis repris au Pérou et en Bolivie. Les résultats de ces formations n'ont pas été analysés à ce jour, mais s'avèrent prometteuses.

Fig. 2 : Photos de la formation basée sur un modèle, dans la province de Bolivar en Equateur. Un plateau représente le paysage agricole (A) où le ravageur se disperse. Les taux d'infestation sont représentés par une gamme de couleurs indiquant la sévérité de l'infestation (B). Chaque agriculteur participant choisit des mesures de contrôle du ravageur à l'aide de cartes à jouer (C). En fonction de ces dernières, le modèle permet de mettre à jour les niveaux d'infestation, puis d'en expliquer la provenance aux agriculteurs à l'aide de jetons (D). Chaque pas de temps est suivi d'une discussion entre participants pour éventuellement modifier les pratiques culturales.

3.3. Propriétés émergentes et analyses des résultats

Dans ce manuscrit, les systèmes sociaux ont été abordés sous forme de variables du paysage (*M1*, *M2*), puis sous forme d'agriculteurs agents diffusant de l'information (*M3*, *M4*), et enfin sous forme d'agriculteurs agents « vecteurs » d'un ravageur des cultures (*M5*). La propriété émergente étudiée dans ce travail était la dynamique spatio-temporelle d'insectes ravageurs des cultures. Néanmoins d'autres propriétés émergentes sous-jacentes auraient pu être mises à jour (*e.g.* formation de barrières à la dispersion des insectes, effets de vagues de diffusion de l'information pour les agriculteurs), si elles avaient été recherchées et étudiées. La définition même de l'émergence, telle qu'utilisée dans ce manuscrit (voir l'introduction), rend cependant son identification difficile. Bien que certains aspects soient pris en compte (*e.g. via* le « *Pattern-Oriented Modeling* », Grimm *et al.* 2005 précédemment cité), l'étude des modèles se limite à la question pour laquelle ils ont été développés. De manière plus large et en accord avec Grimm (1999), si l'approche ascendante n'est pas conçue pour aboutir seule à de nouvelles théories[21], le cycle de leur développement et analyse pourrait néanmoins contribuer à la formulation de questions de recherche y participant. Conscient de la quantité d'information générée par les modèles multi-agents et automates cellulaires (Parker *et al.* 2003), la communauté scientifique participe activement au rapprochement entre outils d'implémentation (*e.g.* NetLogo, Repast Simphony, CORMAS), et outils d'analyses statistiques (*e.g.* Mathematica, R) (Thiele *et al.* 2012). Ce rapprochement est aussi révélateur : malgré les avancées récentes (*e.g.* Thiele *et al.* 2011), les méthodes pour analyser les sorties multiples de ces modèles, restent à développer (Sanchez et Lucas 2002, Thiele *et al.* 2012). Ces mêmes méthodes pourraient ainsi contribuer à une identification plus exhaustive des propriétés émergentes des systèmes représentés.

4. Conclusion générale

Dans un contexte de changements globaux, où les changements que nous opérons sont plus rapides que notre capacité à en comprendre les conséquences (Vitousek *et al.* 1997), le scientifique peut alors se demander si les challenges actuels ne sont pas conduits par l'urgence de la situation, plutôt que par la maturité de la communauté scientifique à aborder de tels sujets d'étude. Le même raisonnement pourrait s'appliquer aux volumes des données collectées au regard de la capacité intégrative sans cesse croissante des ordinateurs (Parker *et al.* 2003[22], *e.g.* « *big data* »). La recherche en modélisation n'aurait-elle pas encore beaucoup

[21] « *bottom-up approaches alone will never lead to theories at the system level* », Grimm 1999
[22] Parker *et al.* 2003 : « *massive advances in computing power have meant that sophisticated tools have become widely used before researchers have had time to consider and develop methods to link these models to data* »

à faire tant sur le plan fondamental qu'au niveau des méthodes, avant de pouvoir prétendre élaborer des scénarios prospectifs pluridisciplinaires utilisables à diverses échelles et niveaux d'organisation ? Pour les systèmes socio-écologiques, la communauté scientifique, qui a déjà souffert d'usages « prédictifs » à mauvais escient (Matthews *et al.* 2007), progresse néanmoins de manière constructive à travers des initiatives d'envergures (*e.g.* Carpenter *et al.* 2012), et la volonté de généraliser de bonnes pratiques de modélisation (Peng 2011).

Par la description des systèmes socio-écologiques andins et leur représentation à travers l'exemple de la dynamique spatio-temporelle d'un insecte ravageur des cultures, ce travail apporte sa contribution en présentant diverses formes de couplage des systèmes sociaux et écologiques, et ce à divers niveaux d'abstraction. Inspiré par les travaux du réseau ComMod[23], ce travail tente également de montrer comment une stratégie de divulgation centrée sur un modèle pourrait bénéficier aux programmes traditionnels de formation en protection intégrée des cultures. Depuis l'acquisition de données écologiques et sociales jusqu'à la formation, ce travail suggère ainsi de repenser et repositionner la modélisation comme une composante intégrative des projets de recherche, et comme un moteur structurant du travail pluridisciplinaire (voir Fig. 3).

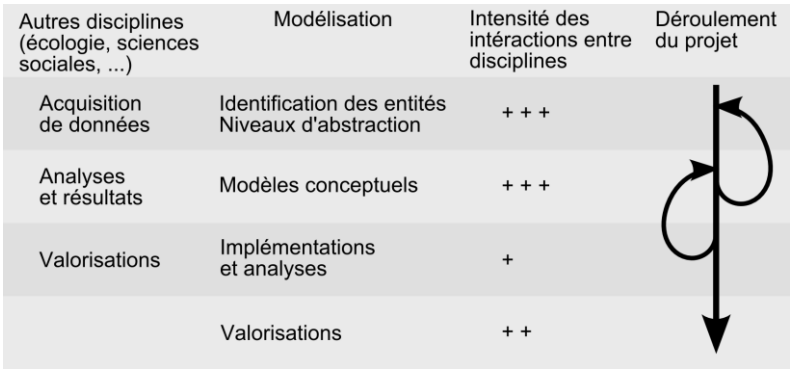

Fig. 3 : Représentation simplifiée des grandes étapes d'une proposition de repositionnement de la modélisation dans les projets de recherche (trop souvent la modélisation n'intervient qu'en fin de projet, tardivement pour identifier les besoins qui auraient pu conduire aux objectifs fixés).

C'est donc en associant de manière étroite le chercheur modélisateur dans la rédaction et la coordination des projets de recherche qu'une avancée vers la compréhension des systèmes socio-écologiques, serait en mesure de répondre aux challenges actuels comme ceux à venir.

[23] ComMod : La modélisation comme outil d'accompagnement (voir http://cormas.cirad.fr/ComMod/)

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ANNEXES

Annexes

1. Modéliser la dispersion d'espèces envahissantes dans un paysage complexe : le cas de la teigne de la pomme de terre en Equateur (Supplementary material)

Appendix S1. Description of the cellular automata basic scenario.

Appendix S2. Description of the storage structure temperature survey.

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 amount of 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

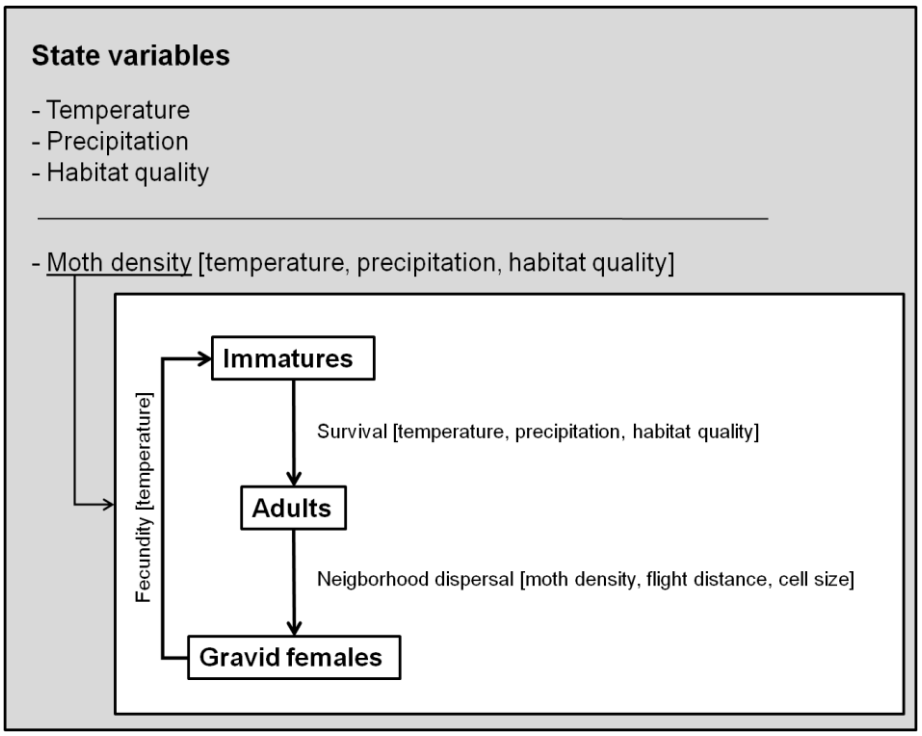

Fig.1. Schematic model structure. Variables in the grey area are the state variables of the model. The white zone represents higher-level variables that contain information deduced from state variables.

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 km²) to fit the level of precision available on the land use data. Elevation, temperature, and precipitation had a 1 km² 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:

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

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.

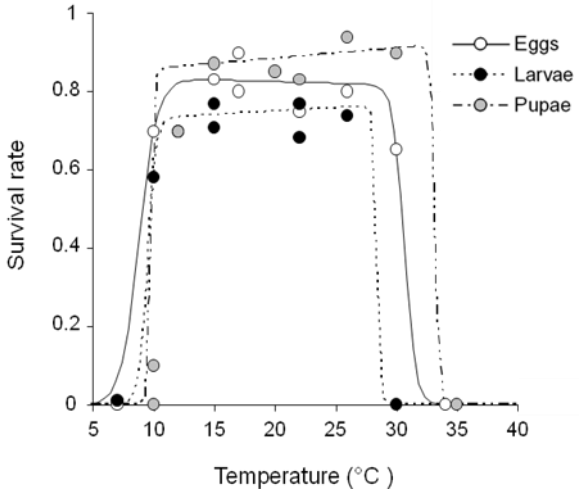

Fig. 2. Effect of constant temperatures on the survival rate *S(T)* of *T. solanivora*'s immature life stages as fitted by eq. 2. Circles represent observed survival rates and lines correspond to the adjusted model.

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):

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

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***	***R²***
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).

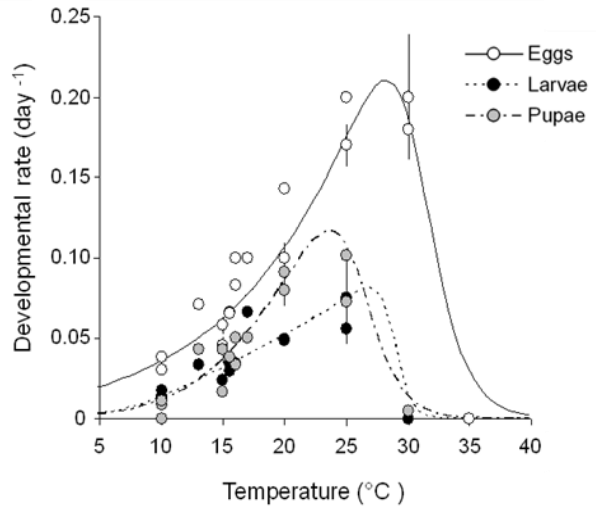

Fig. 3. Effect of constant temperatures on the stage specific developmental rate *D(T)* of *T. solanivora*'s immature life stages. Circles represent observed survival rates and lines correspond to the adjustment of the Sharpe and DeMichel equation (eq. 2).

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).

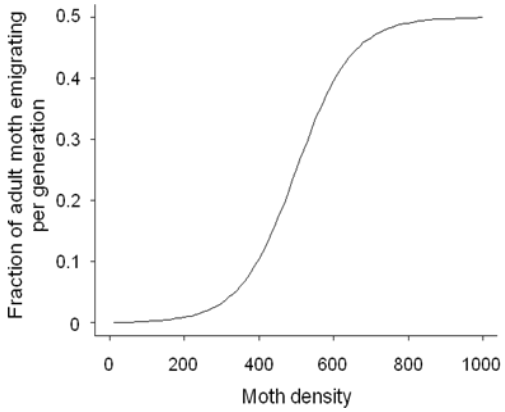

Fig. 4. Fraction of *T. solanivora* adults emigrating as a function of adult density (eq.5). Carrying capacity (K) was fixed to 1000 adults per cell.

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

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

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 β = 500 and ψ = 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:

$$P_{dist} = e^{-\varepsilon * \delta} \qquad (4)$$

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:

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

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 $P_{leaving}$:

$$P_{leaving} = P_{cross} * P_{dist} \quad (6)$$

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

$$N_{disp} = V_{Mi} * P_{leaving} \quad (7)$$

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

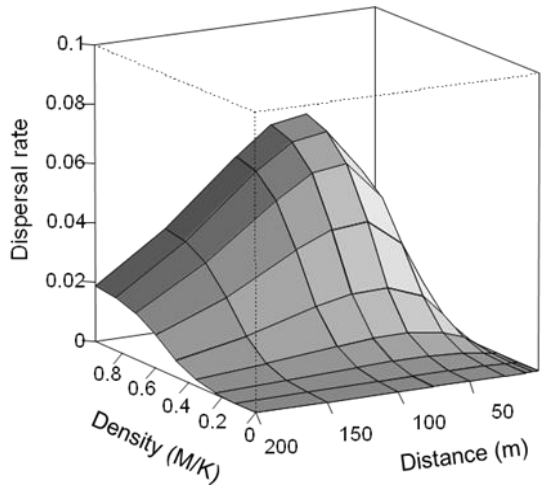

Fig.5. Effective dispersal rate considering moth density and flight distance.

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).

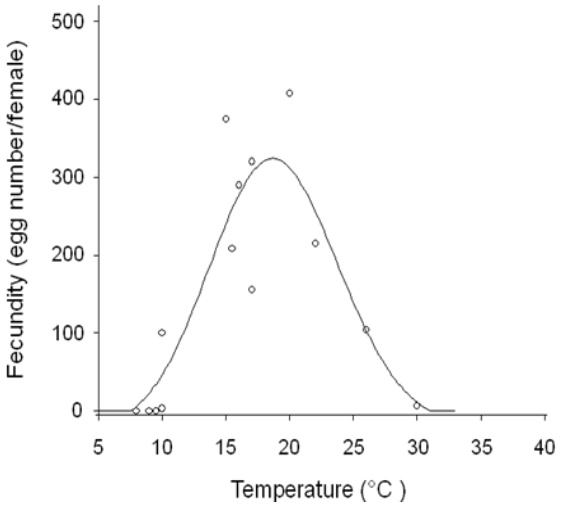

Fig.6. Effect of constant temperatures on moth fecundity *F(T)* as fitted by equation 8.

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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).

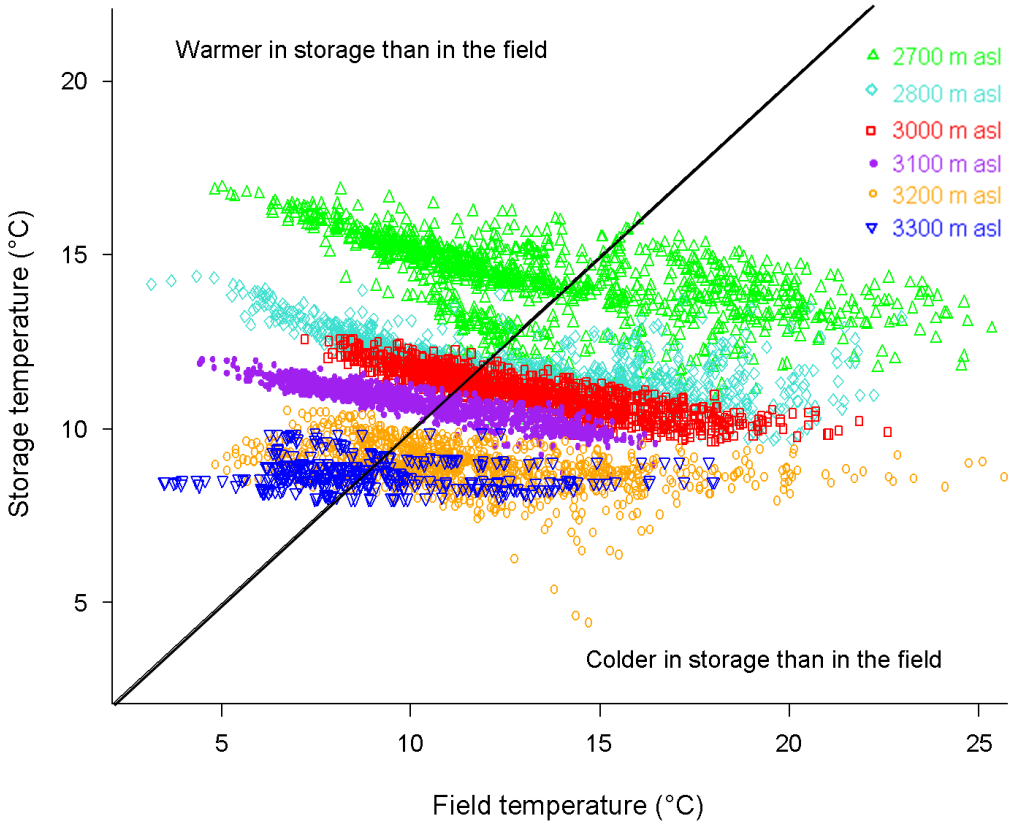

Fig.1. Relationship between storage structure and field temperatures at 6 sites located at different altitudes.

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

2. Un modèle de simulation individu-centré de génétique des populations dans des paysages modifiés par l'homme

Text S1: Supplementary material for online publication only

ODD protocol

The model description follows the ODD (Overview, Design concepts, Details) protocol for describing individual- and agent-based models (Grimm *et al.* 2006, 2010). It is destined to readers looking for a full description and verification of a particular process, but most of all for users willing to modify or extend the code to their own study cases.

To run the model, users need to install NetLogo (wilensky 1999), freely available at http://ccl.northwestern.edu/netlogo/. We used NetLogo 5.0RC6 to build this simulation model.

1. Purpose

Worldwide, populations evolve on various habitats, in which the level of modification or alteration by human activities is heterogeneous. The aim of this model is to study the impact of human activities, through land use, on the structure of populations in order to establish scenarios including changes likely to append in land use or at a broader context, global changes.

2. Entities, state variables, and scales

2.1. Individuals

Each individual in the model represents an entity, characterized by state variables (see Table S1) stored in one global state variable `list_agent` containing the information of all individuals located in a given grid cell. This variable is therefore a list of lists stored for each given cell as a layer. Additional state variables, lineage, habitat type and coordinates are stored in a `list_agent_memory` variable which is updated at each time step and stored in an external file for analysis. Each time step in the model corresponds to one individual generation (non-overlapping) and simulations could run for any number of time steps.

Table S1. State variables of individuals' entities.

State variable names in the code	*Definition*	*Type*
`id_agent`	Number to identify each individual	Integer
`cap_move_def`	Default value for individuals dispersion capabilities	Integer
`cap_fitness_def`	Default value for individuals fitness (number of offspring)	Integer
`list_allele_n`	List of alleles for each neutral locus	List (Integer)
`list_allele_s`	List of alleles for each selected locus	List (Integer)

2.2. Grid cells

As mentioned above, list of all individuals with their characteristics are stored in the `list_agent` variable which is unique for each grid cell. The grid represents the landscape in which the individuals evolve. Each cell is characterized by its state, descriptor of environmental conditions which drive the behavior and dynamics of individuals, composed of a barrier variable representing the cost to move to a given cell (`habitat_barrier`), a resource representing the suitability of a given patch (`habitat_resource`), *i.e.* the carrying capacity and a habitat type representing the characteristics regarding adaptation (`habitat_type`). The cells evolve over time according to management rules. The landscape size is defined in the Graphical User Interface (GUI), see Fig. S1.

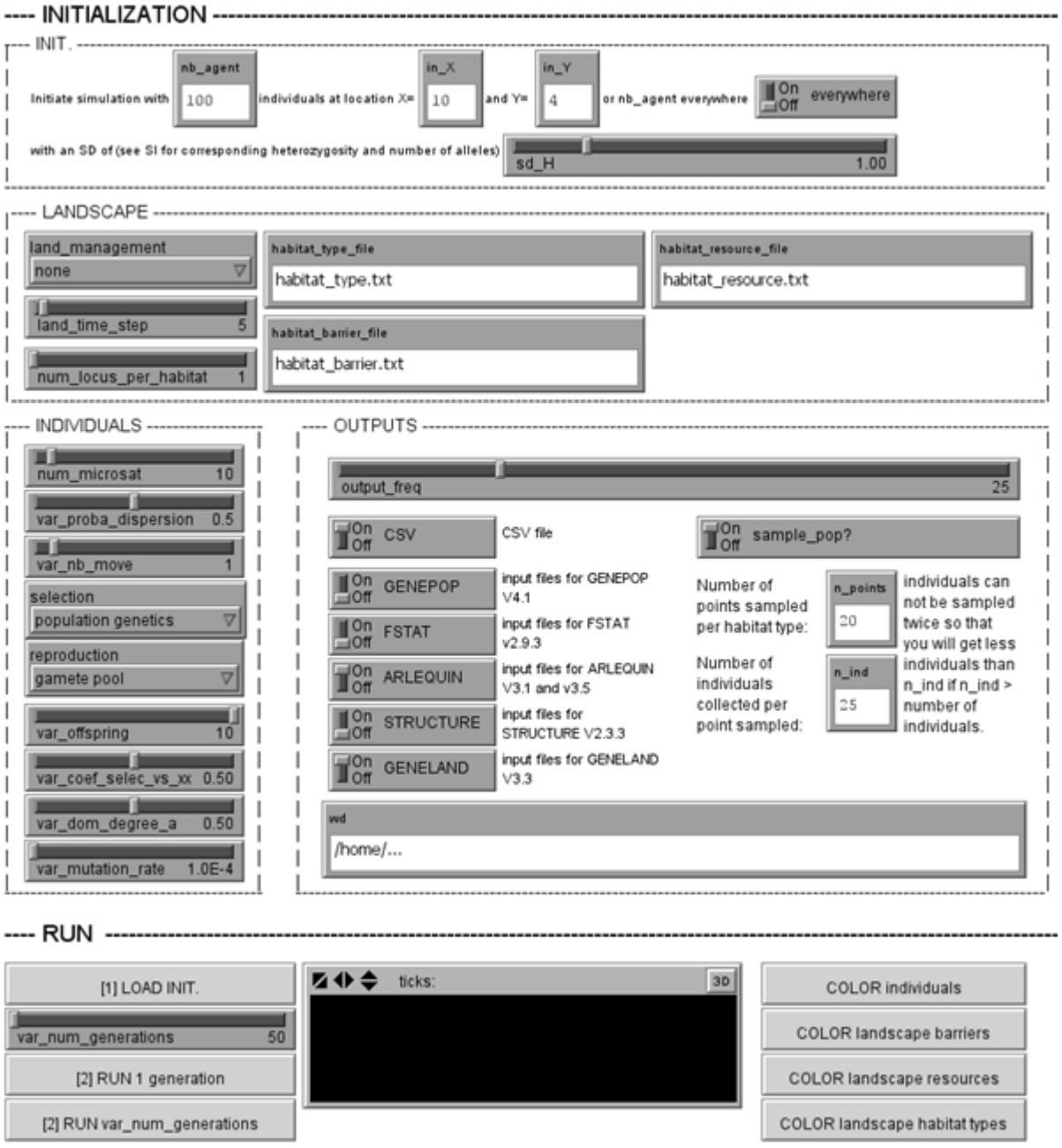

Fig. S1: Graphical User Interface of the simulation model using NetLogo 5.0RC6 (wilensky 1999)

2.3. Collectives

Group of individuals located in the same habitat type are considered as populations for further analysis.

3. Process overview and scheduling

The model processes include the reproduction, survival and dispersion of individuals in this given order for each given cell in a random order. Time is modeled as discrete steps. At the end of one time step, all individuals die, and the next time step begins with their offspring (*i.e.* non-overlapping generations). The information regarding the previous generation after reproduction is stored into the `list_agent_memory` variable. All individuals' state variables are updated synchronously, except for survival where individuals die asynchronously in a randomized way until reaching the carrying capacity.

4. Design concepts

4.1. Basic principles

The model design is based on previous work on the fields of landscape genetics where significant advances have been made on the last decade (Manel *et al.* 2003 ; Manel et Segelbacher, 2009). This simulation model is generic enough to be adapted for all living forms and is based on previous works by Gavrilets *et al.* 2007 and Gravilets and Vose, 2005 for their study on *Cichlidae* ; Duenez-Guzman *et al.* 2009 for their work on *Heliconius* ; Bruggeman *et al.* 2010 and Bruggeman *et al.* 2009 for their work on *Picoides borealis* ; Philips *et al.* 2004 for their work on trees ; Lawson et Jensen, 2005 ; Saledin et Littlejohn, 2003 ; Landguth *et al.* 2010a ; Landguth *et al.* 2010b ; Landguth *et al.* 2010c and Jaquiéry *et al.* 2011 for their generic studies. Our work differ from those for its generic approach with genetic, ecological and landscape submodels with a high level of abstraction allowing to attempt the construction of scenarios rather than explaining a given situation (from real world to theoretical situations). The landscape submodel can run asynchronously with others submodels to reproduce time lags or independent landscape management.

4.2. Emergence

Almost all results of the model emerged from the behavior of the individuals depending on their adaptive traits in the given evolving landscape and were expected to vary in complex ways when particular characteristics of individuals or their environment changed. However initial characteristics of individuals are imposed and hence dependent on what type of individual is simulated, and hence 'built in' rather than emergent results.

4.3. Adaptation

Adaptive traits were considered for all individuals through reproduction. Individuals with a genetic background in favor of a specific habitat are expressing a better fitness than other individuals. Applying Mendel inheritance laws and ecology concept of carrying capacity, the next generation have a higher proportion of individuals with high fitness.

4.4. Objectives

Individuals do not make decisions by ranking alternatives and fitness is a consequence of random move and genetic background. Individuals' objective is to reproduce, which results in the colonization of the landscape.

4.5. Learning
Individuals change their adaptive traits over time as they adapt to a given habitat. These changes occur between generations and not during a time step (*i.e.* no learning). The adaptation is heritable and subject to mutations.

4.6. Prediction
The dispersion of individuals can be considered as a tacit prediction that dispersion to another cell will give to the individuals a better probability of survival.

4.7. Sensing
Individuals perceive their peers in a given cell and the location of potential destinations in their neighborhood (used for dispersion). The mechanisms by which individuals obtain information are modeled explicitly.

4.8. Interaction
Interactions between individuals are direct for reproduction and indirect for mediating resource (carrying capacity). They are no communication between individuals.

4.9. Stochasticity
The survival and mating of individuals in a given cell are modeled randomly to reproduce variability and because we assumed that actual causes of the variability were unimportant given the model objectives. The dispersion of individuals is random among possible destinations because we assumed that individuals do not have a perception of habitats located in other cells.

4.10. Collectives
Individuals in a given habitat belong to an aggregate named population. Population is the result of adaptation and dispersion. Population genetics analyses are made at this defined level.

4.11. Observation
All information regarding individuals can be collected for analyzing the model after each reproduction process (*i.e.* at each time step). This information can also be sampled and used to imitate what can be observed in an empirical study (see the "Virtual Ecologist" approach by Zurell *et al.* 2010, as mentioned by Grimm *et al.* 2010).

5. Initialization

The initial state of the model (*i.e.* at time $t = 0$) is composed of a user-defined number of individuals located in the landscape. Alleles at both the selected and neutral loci are initialized randomly and consequently vary among simulations. In this simulation model, consequences of initial state are studied so that user-defined initialization is of importance in order the results to be accurately replicated. Default values are provided in Table S2

Table S2. Default values at initialization.

Variable names	*Definition*	*Default value*
INIT.		
nb_agent	Number of individuals per cell	100
in_X	X Coordinate of individuals	20
in_Y	Y Coordinate of individuals	4
everywhere	To specify that individuals are located in every cells	False
Sd_H	Standard deviation of the normal distribution defining the number of alleles and heterosygosity among the population	1
LANDSCAPE		
land_management	Type of land management	None
land_time_step	Time steps for land management	5
num_locus_per_habitat	Number of selected loci per habitat type	1
habitat_type_file	Name of the file containing habitat types	"*habitat_type.txt*"
habitat_barrier_file	Name of the file containing habitat barriers	"*habitat_barrier.txt*"
habitat_resource_file	Name of the file containing habitat resources	"*habitat_resource.txt*"
INDIVIDUALS		
num_microsat	Number of microsatellites loci	10
var_proba_dispersion	Dispersion rate	0.5
var_nb_move	Number of movements	2
selection	Type of selection submodel	Population genetics
reproduction	Type of reproduction submodel	Gamete pool
var_offspring	Offspring	10
var_coef_selec_vs_xx	Selection coefficient against the deleterious genotype	0.5
var_dom_degree_a	Degree of dominance of the deleterious allele	0.5
var_mutation_rate	Mutation rate	10^{-4}
OUTPUTS		
output_freq	Outputs frequency (every *x* time steps)	10
CSV	Comma-separated values output	True
GENEPOP	Genepop output	True
FSTAT	Fstat output	True
ARLEQUIN	Arlequin output	True
STRUCTURE	Structure output	True
GENELAND	Geneland output	True
sample_pop?	Sample over outputs	True
n_points	Number of points per habitat type	15
n_ind	Number of individuals per point sampled	50
wd	Directory for outputs	/home/…

6. Input data

The simulation model uses external sources for the integration of the landscape layers (GIS). These files concern the landscape habitat ("*habitat_type.txt*"), the landscape resource ("*habitat_resource.txt*") and the landscape barrier ("*habitat_barrier.txt*"). Fig. S2 represents an example of input data file at initialization for habitat types. If no files are provided, the model will run with default values of 1, 1000 and 10, respectively. Each file is organized with coordinates in the first two columns and landscape characteristic in the third as following:

0 0 1
1 0 4
…
10 10 3

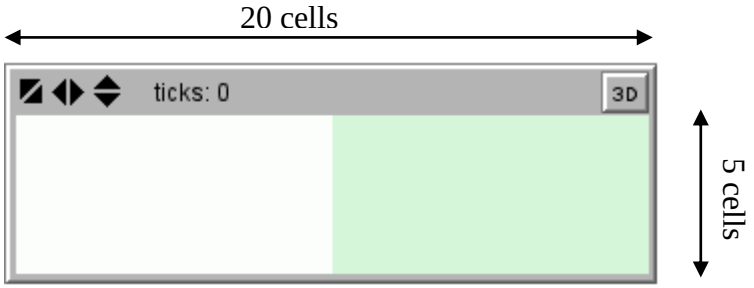

Fig. S2: Graphical representation of an example of habitat types at initialization

Alleles are chosen in a normal distribution with a user-defined standard deviation `sd_H` corresponding to an expected number of alleles and rate of heterosygosity (See Fig. S3). For example, when `sd_H` = 1, the expected heterosygosity is around 70% and the number of possible alleles lesser than 10.

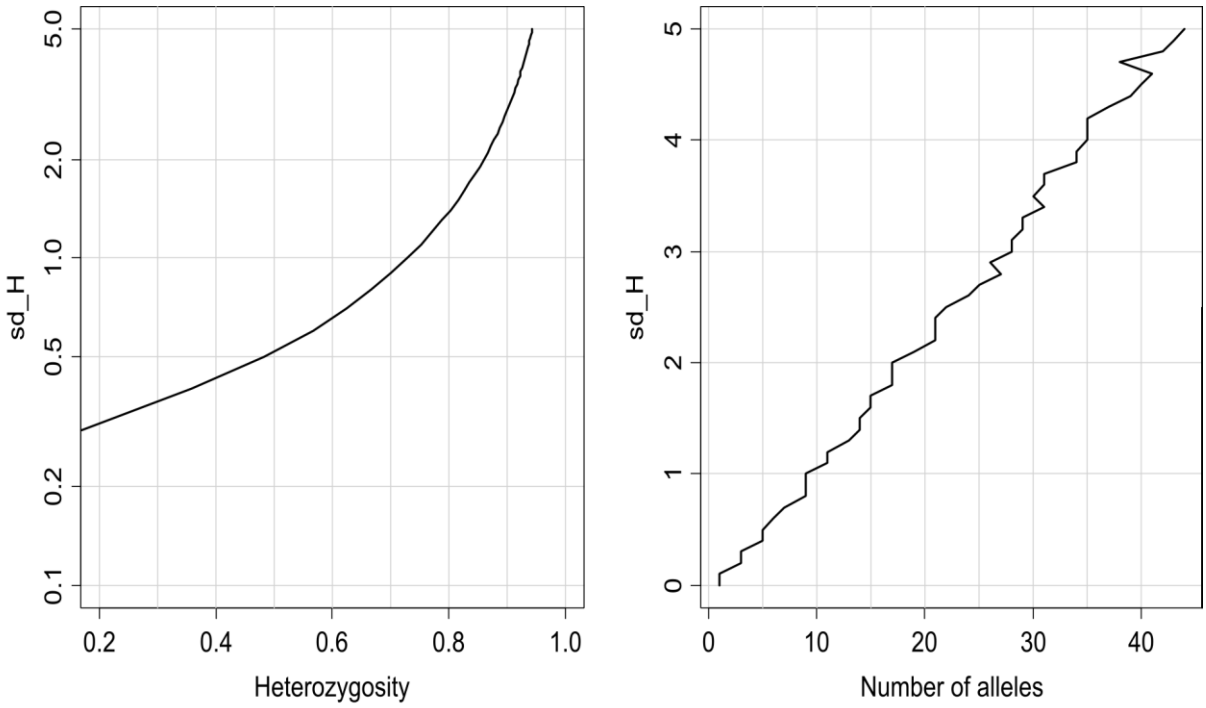

Fig.S3: Heterosygosity and number of alleles corresponding to the parameterization of sd_H in the GUI, using 10000 random values in a normal distribution

7. Submodels

7.1. Individuals related submodels

7.1.1. Reproduction (`agent_reproduce_genpop`)

Description

The reproduction submodel is based on the assumption that all individuals located in a given cell have a probability of mating, and that mating occurs as if all gametes were chosen in the population (*i.e.* gamete pool) with a probability defined by individuals' relative selective values. Then transmission of genetic characteristics follows Mendel inheritance laws. The number of descendants is defined by the individual variable `var_offspring` adjusted according to fitness traits depending on the habitat type (`habitat_type`). The population genetics submodel is detailed in the main text and not copied in this supplementary material. Mutations occur only in microsatellites loci with a probability of 10^{-4} which can be modified through the GUI.

Validation

The population genetics submodel is based on Hartl (2005), Wade *et al.* (2001) and Trajstman (1973). We assumed a stepwise mutation model as defined by Hamilton (2009, p 169).

Verification

In the code the relative selective values w_i of each individual is stored in a list (`allwi` in procedure `agent_set_wi_genpop`) which also contain all individuals identification number. Then two gametes are chosen in the gamete pool with a probability based on w_i so that selection is conserved. The selection of two gametes is reproduced *f* times for the creation of the next generation. This submodel has been checked by verifying that selection was operational over a large number of individuals with a broad range of selection coefficients. To verify that Mendel inheritance laws were adequately reproduced by our model, we simulated more than 1000 first generations with a marked gamete and checked the allele frequencies of 10 loci (allele frequency of 0.49995, CI95% = [0.4952743 ; 0.5046257]).

```
Pseudo-algorithm
FOR all cells {
     IF at least 2 individuals {
          define number of offspring f
          REPEAT f times {
               choice into gamete pool (probability wi)
               create descendant with Mendel inheritance laws
          }
     }
     remove old generation of individuals
}
```

7.1.2. Survival (`agent_survival_alt`)

Description

Each cell in the grid is characterized by a carrying capacity defining the maximum number of individuals that a cell can contain (variable `habitat_resource`). When the number of individuals is higher than the carrying capacity, individuals are randomly removed until the carrying capacity is reached.

Verification
This submodel has been checked by verifying that the number of individuals after removal corresponded to the carrying capacity, then by verifying that the individuals were properly removed, and finally by verifying that the selection of individuals was properly randomized.

Pseudo-algorithm
```
FOR all cells {
     WHILE number of individuals > carrying capacity {
          remove randomly individuals from the cell
     }
}
```

7.1.3. Dispersion (agent_dispersal_alt)

Description
Each individual can move from one cell to another located in its Moore neighborhood. Each cell is characterized by its resistance (patch variable `habitat_barrier`). Lowest values of resistance represent easy to cross cells and highest values impermeable cells. On the other side, each individual is characterized by its dispersion capabilities (individual variable `cap_move`). Consequently, an individual with higher dispersion capabilities could move to more cells within its Moore neighborhood (see Fig. S4).

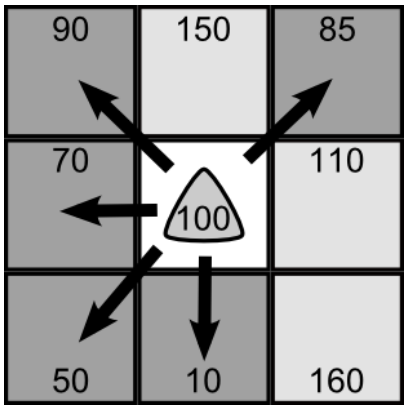

Fig. S4. Individual potential destinations. An individual is located in the central cell with a dispersion capability of 100. Potential destinations are represented in dark grey.

The decision whether to move to another cell is based on a fixed probability (default probability of 0.5). The destination cell is chosen randomly among potential destinations.

Validation
We assumed that individuals do not have a perception of the suitability of neighboring cells and disperse randomly into the landscape.

Verification
This submodel has been checked by verifying that the number of individuals selected for dispersal corresponded to the rate of dispersion, by verifying that the potential destination cells were adequate to dispersal capabilities, that the individuals moving were properly removed from the buffer list, and finally that individuals were properly relocated to chosen destinations.

Pseudo-algorithm
```
FOR all individuals {
```

```
   WHILE individual can move {
      list of potential destinations
      movement to a random cell among potential destinations
      update of dispersal capacity according to movement
   }
}
```

7.2. Initialization related submodels

7.2.1. Setting up the list of alleles for neutral and selected loci

Each allele for microsatellites loci are chosen randomly in a range of integers from 1 to `allelic_richness` (according to `heterozigosity` rate), and selected alleles randomly between 0 and 1.

7.2.3. Setting up the individuals

Identification numbers are incremented during the reproduction process and for the entire simulation. Number of alleles and heterosygosity are presented in section "input" (see Fig. S3).

7.3. Landscape related submodels

7.3.1. Landscape generation

External files:

- "*habitat_type.txt*" for the landscape habitat type,
- "*habitat_resource.txt*" for the landscape carrying capacity and
- "*habitat_barrier.txt*" for the landscape resistance.

In case files contain errors, a default value is attributed to each layer.

7.3.2. Landscape management

Landscape can change over time due to human actions. The simulation model includes a landscape management submodel that reproduces various scenarios.
Alternatives are:

- "none" no landscape management
- "random" random changes over time
- "neighbor4" changes to one of the 4 neighbors
- "neighbor8" changes to one of the 8 neighbors
- "emergence" changes to a new habitat type
- "user-defined" to let the user program his own submodel

7.4. Output

Description
In order to perform population genetics analysis, the simulation model produces outputs for the most-used population genetics software (see Table 1 in the main text). The sampling method is based on random location and random individuals.

Validation
The choice of software was realized following Excoffier and Heckel 2006.

Verification

Each output has been checked using the corresponding software.

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3. La modélisation multi-agents : un outil pour définir des stratégies de lutte contre les ravageurs dans des communautés hétérogènes d'agriculteurs

Appendix A: Model description using the ODD protocol

The model description follows the ODD (Overview, Design concepts, Details) protocol for describing individual- and agent-based models (Grimm *et al.* 2006, 2010).

A1. Purpose

The model is a combined cellular automaton (CA) and agent-based model (ABM) designed to explore the consequences of farmer's agricultural practices on insect pest infestation levels during a simulated IPM extension program. In this paper, the model was used in the specific scope of exploring the role of the type of IPM information diffusion (passive *vs.* active) and farmers' heterogeneity in IPM receptivity to control an emergent pest. The model simulates pest population spread, information diffusion, and system sustainability (pest infestation levels) and was used to explore the effect of agent heterogeneity in information diffusion and effective strategies to improve actual IPM programs. The model was developed using NetLogo (Wilensky 1999).

A2. Entities, state variables, and scales

Entities, state variables and scales are summarized in Table A.1.

A2.1. Environmental entities

The landscape in the model is divided into *n* farms characterized by their height and width in cells (2 × 3 cells, each cell corresponding to a field *z*). The total area covers 20 × 30 cells.

A2.2. Spatial unit entity

Each cell of the grid can be infested by a pest attributing to the cell a pest infestation level. The pest entity is characterized by its carrying capacity *K*, an inoculums *I*, a dispersal rate *d*, a growth rate *r*, its spatial coordinates within the grid, and its level of infestation (from 0 to *K*).

A2.3. Agent entity

Agents simulate farmers in the landscape and are attributed to each farm (one agent per farm). Each agent *i* is characterized by a social network range *s*, a level of knowledge regarding IPM practices named IPM information *k*, a receptivity rate *r* representing its attitudes towards the IPM practices itself simulated by a random number in a normal distribution *N*(*mu*, *sd*), a pest

control level prior to gain IPM information c_{init}, a pest control level as a function of IPM information (auxiliary variable c_{IPM}), a way to diffuse the information *f* (active or passive), a number of diffusion events per time step *ev*, a number of action per time step *evt*, and a location within its farm.

A2.4. Scales

One time step in the model represents one pest generation.

A3. Process overview and scheduling

A3.1. Spatial distribution of the pest and ecological rules

At each time step, pest infestation is updated using a logistic growth equation (see 7.1.). Then the pest disperses into the neighborhood cells of the grid.

A3.2. Agents diffusion of the innovation and pest control

Agents sense the pest infestation level in their fields and the IPM information of agents in their social network. This sensing capability allows them to choose among two behavioral alternatives: controlling the pest using their own IPM knowledge or interacting with other agents to learn/teach about IPM practices. If agents choose to control the pest, it is applied only to the field they occupy. After each action performed agents move randomly within their farm.

A4. Design concepts

A4.1. Basic principles

The pest model uses the classical logistic growth function developed by Pierre Verhulst (1838) who suggested that the rate of population increase may depend on population density. The farmer behavior model follows two main theories of diffusion of information (active and passive).

A4.2. Emergence

The pest infestation in agents' fields emerges from ecological rules (logistic growth and dispersion) and from agents' behaviors which itself emerges from IPM information diffusion.

A4.3. Adaptation

Agents adapt their behavior depending on the pest infestation level in their fields, their receptivity towards the IPM practices, and their social network.

A4.4. Objectives

Agents' main objective is to decrease pest infestation on their land, thereby implicitly increasing their crop production and incomes.

A4.5. Learning

As agents learn from others, they increase their IPM information and capacities to control the pest control. This occurs at two levels: 1) in their own farm and 2) in the whole community of agents as they can train other agents to better control pest on their farm (either actively or passively).

A4.6. Prediction

The tacit prediction of our model is that by participating to the diffusion of IPM information (either actively or passively) agents would reduce pest infestation events from neighboring fields, therefore meeting their main objective.

A4.7. Sensing

Agents perceive pest infestation level on their own farm. They also perceive (within the range of their social network) both location and IPM information of other agents in the community. We assumed that an agent A1 can perceive the IPM information of an agent A2 thanks to observation of pest infestation in A2's farm.

A4.8. Interaction

Agents interact directly through informal IPM training sessions (at the helper or helped agent initiative depending on IPM information diffusion type). Interactions are local, *i.e.* within a range of cells defined by their social network size.

A4.9. Stochasticity

Stochastic factors are included in agents' movement within their farm and in the order they performed actions.

A4.10. Collectives

There is no intermediate level of organization in the ABM apart from farms which constitute aggregates of 6 cells (fields).

A4.11. Observation

Two types of data were generated by our model: IPM information of agents and pest infestation levels. These data were collected at each time step and stored into external files.

A5. Initialization

At time t = 0, the pest infestation is fixed to the carrying capacity *K*. All agents have an IPM information of 0, except one, that we assume to have been trained by an external source (as it occurs during extension programs such as farmer field schools, see Van den Berg and Jiggins, 2007). This agent has an IPM information of 5 and is randomly chosen among all agents. The initial values of other variables included in the model are listed in Table A1.

A6. Input data

The model does not use input data to represent time-varying processes.

A7. Sub-models

A7.1. Pest reproduction

The pest reproduction is simulated using a logistic growth function classically used in quantitative ecology with a growth rate *r* and a carrying capacity *K* (see Eq.A1)

$$N_t = \frac{(K . N_0)}{(N_0 + (K - N_0).\exp^{(-r.t)})} \qquad \text{Eq.A1}$$

where N_t represents number of individuals at time *t* and N_0 the number of individuals at time t = 0.

A7.2. Pest dispersion

Pest dispersion to neighborhood fields is simulated using the NetLogo function "diffuse4" (Wilensky, 1999), which allows to disperse the pest into the Von Neumann neighborhood cells using a fixed dispersal rate.

A7.3. Agents' behavioral decisions

A7.3.1. Decision-making

In our model, agents choose among two decision alternatives: 1) they dedicate all their time to control the pest or 2) they share their time in equal proportion between pest control and IPM information sharing with other agents. To perform this decision, we made agents able to perceive short-term benefits of their action. Technically, agents minimize a function N_t, which represents the perceived pest infestation level *N* at a given time *t*. In our case we chose *t* = 1 (*i.e.* one time step) to simulate short term benefices. We assumed that:

$$N_1 = (1 - c) N_0 + i - e \qquad \text{Eq. A2}$$

with *c* the pest control coefficient in farmer's field, *i* the proportion of pest immigrating to farmer's field from neighboring fields (see Eq. A3a for alternative 1 and Eq. A3b for alternative 2), and *e* the proportion of pest emigrating from farmer's field to neighboring fields (see Eq. A4). In the first alternative agent will perceive $i > e$ (they will receive high number of pests from their neighbors) while in the second alternative they will assume that $i = e$.

$$i = N_0 . d \qquad \text{Eq. A3a}$$

$$i = (1 - c) N_0 . d \qquad \text{Eq. A3b}$$

$$e = (1 - c) N_0 . d \qquad \text{Eq. A4}$$

After some model iterations most agents should converge towards the same maximum IPM information but some agents may remain unreceptive to information sharing.

A7.3.2. Passive IPM information diffusion

In our model, passive IPM information diffusion between two agents (considering an agent *a* who wants to increase its IPM information from an agent *b*) could occur if the three following conditions were fulfilled:

- Agent *b* belongs to the social network of agent *a*
- The IPM information level of the agent *a* is lower than that of agent *b*
- Both agents can spend time in to share IPM information (*i.e.* their time credit >0)

If several agents meet these criteria, agent *a* chooses one of them randomly.

Then the probability of agent *a* to learn from another agent is given by Eq. A.5.

$$P(success) = p_{ia} * r_a \qquad \text{Eq. A.5}$$

where p_{ia} is the pest infestation in the farm of agent *a* and r_a the receptivity of agent a (see the main document for further details).

A7.3.3. Active IPM information diffusion

In our model, active IPM information diffusion between two agents (considering an agent *a* who wants to increase the IPM information level of an agent *b*) could occur if the three following conditions were fulfilled:

- Agent *b* belongs to the social network of agent *a*
- The IPM information level of the agent *a* is higher than that of agent *b*
- Both agents can spend time in to share IPM information (*i.e.* their time credit >0)

If several agents meet these criteria, agent *a* chooses one of them randomly.

Then the probability of the given agent to teach to the other is given by Eq. A.6.

$$P(success) = p_{ia} * r_b \quad \text{Eq. A.6}$$

where p_{ia} is the pest infestation in the farm of agent *a* and r_b the receptivity of agent *b*.

A7.3.4. Pest control

Agents dispose of 6 fields on their farms. During each time step they move randomly and decide to perform either "control" or "sharing information" actions. Based on field results obtained by the authors in another study (Rebaudo and Dangles 2011) pest control by agents c_{IPM} was expressed as a linear function of IPM information level using Eq. A.4.

$$c_{IPM} = 0.2 * k \quad \text{Eq. A.7}$$

where *k* is the IPM information level ranging from 0 to 5.

A7.4. Agents' movement

Agents moved randomly within their farm after each action performed.

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Table A1. Entities and state variables used in the model. Values in square brackets represent ranges of possible values.

Entity	Entity type	State variables	Scales and initialization
Landscape	Environment	Height	20 cells
		Width	30 cells
Farm	Environment	Height	2 cells
		Width	3 cells
Pest	Spatial	Carrying capacity	$K = 1$
		Inoculums	$I = 1$
		Dispersal rate	$d = 0.5$; [0:1]
		Growth rate	$r = 1$
		Spatial coordinates	$(x;y)$
		Pest infestation	$p = [0:K]$
Farmer agent	Agent	IPM information	$k = [0:5]$
		Social network range	$s = 3$; [1:10]
		IPM receptivity	$r = N\sim(mu_i, sd_i)$
		Mean receptivity	$mu = 0.5$
		Standard deviation receptivity	$sd = 0.5$; [0:1]
		IPM pest control	$c_{IPM} = [0:1]$
		Information diffusion type	$f =$ [active; passive]
		Diffusion events per model step	$ev = 3$
		Events per model step	$evt = 6$
		Location within farm	$(x;y)$

Appendix B: Supporting information: statistics of the validation of our ABM using the Bass model

This appendix contains additional analyses supporting the main text.

Table B.1. Statistics for the active IPM information diffusion fit to the Bass model. Residual standard error: 0.5873 on 97 degrees of freedom, Number of iterations to convergence: 12, Achieved convergence tolerance: 6.906e-06

Formula	DiffEvents ~ M * (((P + Q)^2/P) * exp(-(P + Q) * time))/(1 + (Q/P) * exp(-(P + Q) * time))^2			
Parameters	**Estimate**	**Std. Error**	**t value**	**Pr(>|t|)**
M	2.935e+02	8.329e+00	35.24	<2e-16
P	6.343e-03	3.766e-04	16.84	<2e-16
Q	3.584e-02	2.495e-03	14.37	<2e-16

Table B.2. Statistics for the passive IPM information diffusion fit to the Bass model. Residual standard error: 1.127 on 97 degrees of freedom, Number of iterations to convergence: 14, Achieved convergence tolerance: 5.429e-06

Formula	DiffEvents ~ M * (((P + Q)^2/P) * exp(-(P + Q) * time))/(1 + (Q/P) * exp(-(P + Q) * time))^2			
Parameters	**Estimate**	**Std. Error**	**t value**	**Pr(>|t|)**
M	4.082e+02	9.696e+00	42.10	<2e-16
P	1.528e-02	8.127e-04	18.80	<2e-16
Q	7.072e-02	4.308e-03	16.42	<2e-16

Appendix C: Supporting information: effect of social network range and pest dispersion capabilities on pest control strategies

This appendix contains additional analyses supporting the main text.

We tested different proportions of agents with active and passive IPM information diffusion (from 0 to 1), with an insect dispersal rate ranging from 0 to 1 (Fig.C1) and a social network ranging from 1 to 10 (Fig.C2). Mean pest infestation level over the community was observed and represented by a color gradient. These complementary analyses did not significantly influence the conclusions drawn from Fig.5 regarding IPM information diffusion strategies. We then tested the effect switching from one strategy to another (active to passive or passive to active) during a simulation between time steps or within time steps.

Fig. C1. Effect of combined insect dispersal rate and proportion of IPM information diffusion type (active *vs.* passive) on mean pest infestation levels in the community at time t = 100 steps. On the Y scale, a proportion of 0.2 means 20% of passive and 80% of active IPM information diffusion. A total of 121 couples of values (insect dispersal rate; proportion of diffusion type) were simulated 100 times and were averaged to obtain mean pest infestation levels in the community (represented by a color gradient ranging from 0 to 1).

Fig. C2. Effect of combined social network and proportion of IPM information diffusion type (active *vs.* passive) on mean pest infestation levels in the community at time t = 100 steps. On the Y scale, a proportion of 0.2 means 20% of passive and 80% of active IPM information diffusion. A total of 110 couples of values (social network; proportion of diffusion type) were simulated 100 times and were averaged to obtain mean pest infestation levels in the community (represented by a color gradient ranging from 0 to 1).

Fig. C3. Effect of combined agents' heterogeneity and proportion of IPM information diffusion type (active vs. passive) on mean pest infestation levels in the community at time t = 100 steps when agents can change of strategy during the simulation. On the Y scale, a proportion of 0.2 means 20% of passive and 80% of active IPM information diffusion. In (A), agents can change of strategy between time steps and in (B), within time steps. The pest infestation levels presented here are the mean of 100 simulations. In both cases the mixed strategy resulted in intermediate pest infestation levels between only passive or only active diffusion strategies.

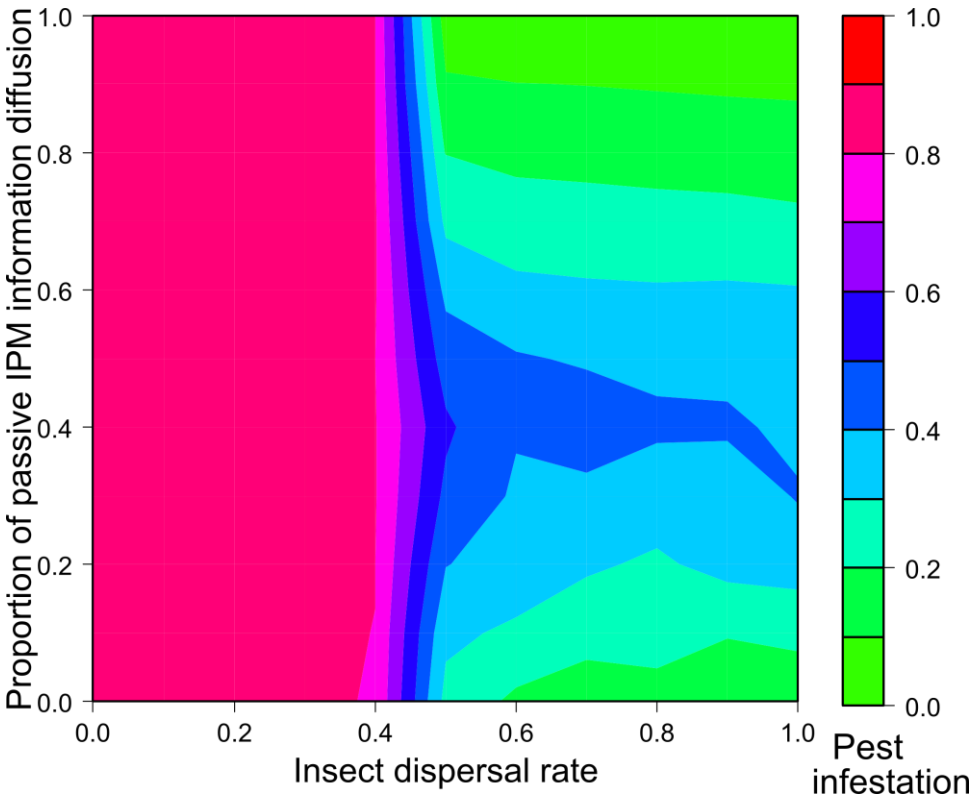
Proportion of passive IPM information diffusion
1.0
0.8
0.6
0.4
0.2
0.0
0.0
0.2
0.4
0.6
0.8
1.0
Insect dispersal rate
Pest infestation

Fig.C1

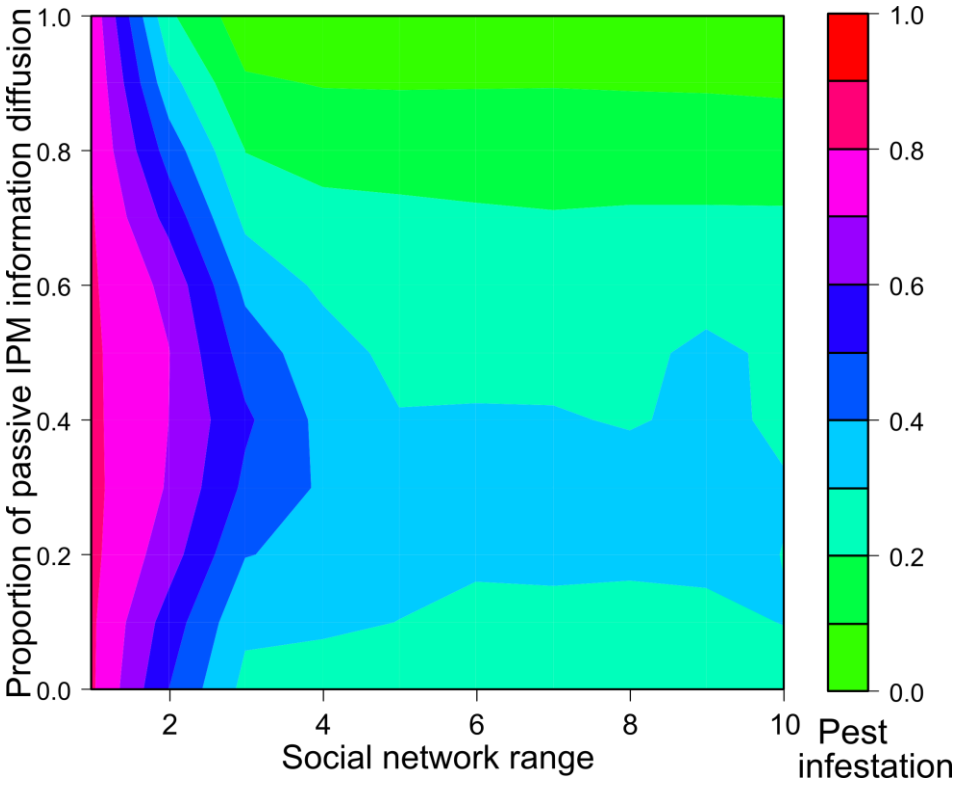
Proportion of passive IPM information diffusion
1.0
0.8
0.6
0.4
0.2
0.0
2
4
6
8
10
Social network range
Pest infestation

Fig.C2

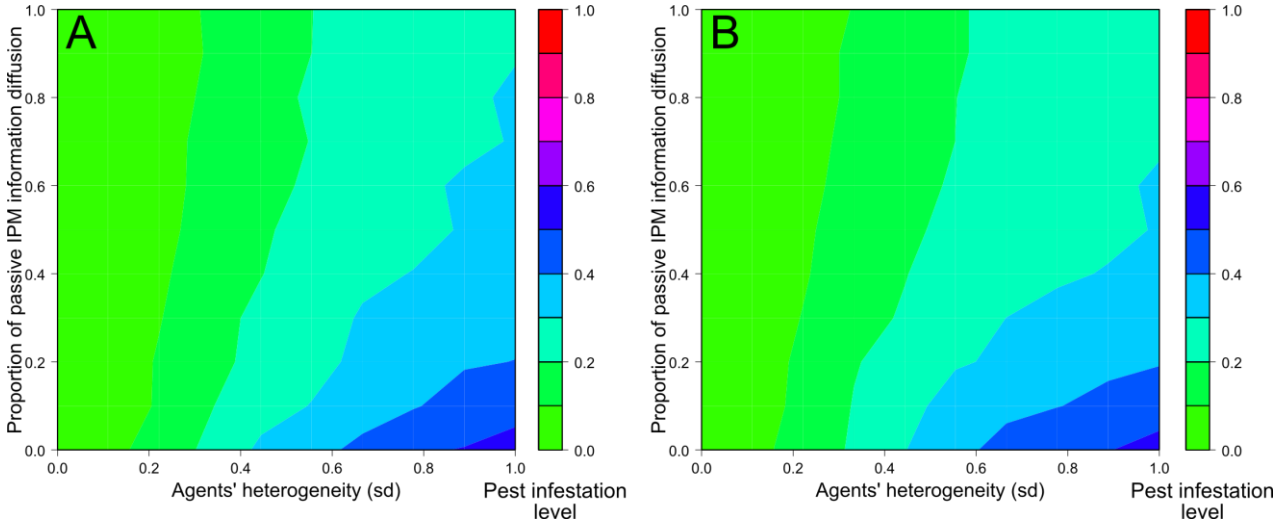
A
B
Proportion of passive IPM information diffusion
Agents' heterogeneity (sd)
Pest infestation level
0.0
0.2
0.4
0.6
0.8
1.0

Fig.C3

Appendix D: Supporting information: results of the effect of IPM information diffusion attenuation on pest control

This appendix contains additional analyses supporting the main text.

Fig. D1. Sensitivity analysis of the effect of an attenuation factor of IPM information diffusion on pest infestation levels, for both passive (A-D), and active (E-H), IPM information diffusion. Mean pest infestation levels are represented over time for five values of attenuation factors for different levels of agents' heterogeneity (sd = 0; 0.25; 0.5; 0.75). Each curve is the mean of 100 simulations during 100 time steps.

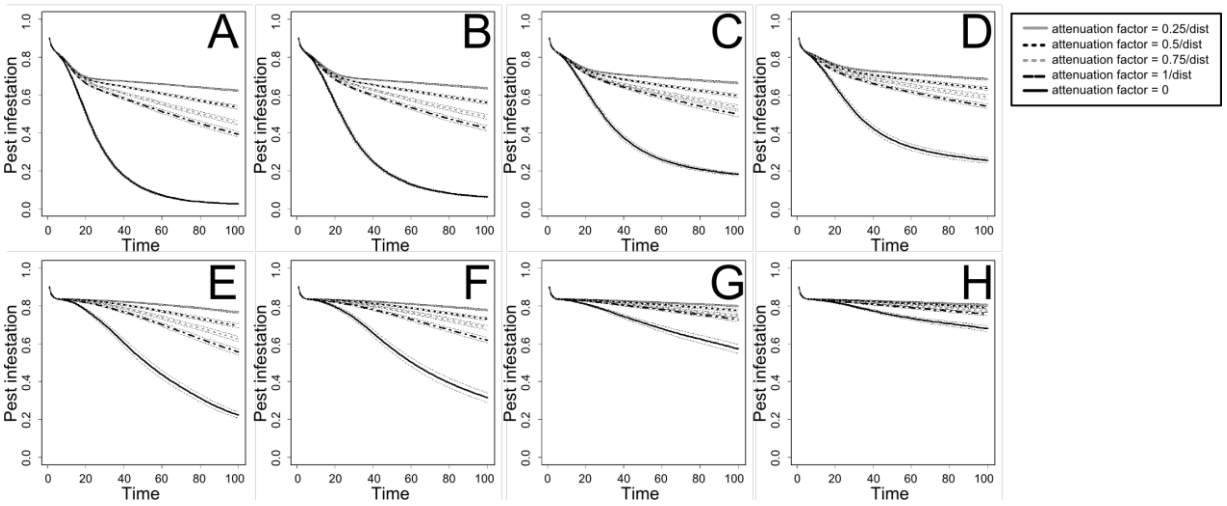

Fig.D1

4. Le couplage d'un modèle de diffusion de l'information avec un modèle de dynamique des populations d'insectes : conséquences pour les agriculteurs dans leur stratégie de contrôle (Supporting Information)

Protocol S1

Source code of the model. The source code was written using CORMAS (March 2008 release) developed with the non-commercial version of VisualWorks® from Cincom Systems.

http://www.ploscompbiol.org/article/fetchSingleRepresentation.action?uri=info:doi/10.1371/journal.pcbi.1002222.s001

Protocol S2

Source code of the model (additional environmental file).

http://www.ploscompbiol.org/article/fetchSingleRepresentation.action?uri=info:doi/10.1371/journal.pcbi.1002222.s002

Text S1

Extended materials and methods. This document includes empirical field data, a model description and model analysis: verification and validation.

Extended materials and methods

1. Empirical data on Andean farmer behaviors

To mimic real-world patterns of farmer behaviors as closely as possible, our ABM was built on farm-level empirical survey data from nationally representative samples of rural Ecuador. Our database was obtained through a three-year household survey conducted in 2006-2008 in four provinces of the Ecuadorian highlands (Bolivar, Tungurahua, Cotopaxi, and Chimborazo) using standard household survey techniques [1]. Survey zones had not been covered by any educational program regarding potato moth management. In total, 293 potato grower families from about 100 different communities were interviewed, gathering data on integrated pest management (IPM) knowledge in communities, levels of pest control, and the efficiency of IPM learning and diffusion processes.

To explore the profitability of IPM program as a function of the coupled dynamics of agent and pest population, we needed three pieces of field information (see Fig. 2 of the main document):

1) Initial IPM knowledge of each agent. To establish the initial IPM knowledge of each agent in the community, each potato grower family of our survey was asked 20 questions, 10 on basic issues (biology and ecology of the potato moth) and 10 on applied issues (potato moth management [2]). Farmer responses to these questions allowed us to establish IPM knowledge scores (ranging from 0 to 5). These data were implemented in our ABM to set up the baseline proportion of the different knowledge scores for the agents.

2) Relationship between IPM knowledge and pest control. For 83 of the 293 interviewed households, we quantified the effect of natural *T. solanivora* larvae infestation on potato plants at harvest time as a proxy of pest control. We determined damage levels for 10 plants in the center of the field by inspecting every tuber for damage by the pest. We then

plotted the IPM knowledge of farmers *vs.* a pest control index calculated on the field pest infestation level.

3) Efficiency of IPM information diffusion between graduate and exposed agents. To measure the magnitudes of IPM learning spillovers from graduate to exposed farmers, we compiled data collected from farmer field school (FFS) events involving a total of 64 farmers conducted in a total of 5 communities [2, 3]. FFS is a form of adult education based on the concept that farmers learn optimally from field observation and experimentation. It was developed to help farmers tailor their IPM practices to changing ecological conditions. In regular sessions, groups of neighboring farmers perform simple experimentation which helps them further improve their understanding crop ecosystem functioning. In this learning process, farmers develop the expertise that enables them to make their own crop management decisions. Special group activities encourage learning from peers, and strengthen communicative skills and group building [24].

The methodology (described in detail in the references mentioned above) consisted in training 10-17 farmers in each community on IPM for *T. solanivora*. Both theoretical and practical training sessions were performed weekly or biweekly based on farmers' convenience during at least three months. At the end of the sessions, all FFS graduates were encouraged to share their knowledge and learning experience with other farmers within their community. IPM knowledge about *T. solanivora* was assessed using a 20-item questionnaire 1) with community members before the FFS (control), 2) with graduate farmers after the FFS, and 3) with exposed farmers after the FFS.

2. Model description

The model description follows the ODD (Overview, Design concepts, and Details) protocol for describing individual- and agent-based models [4-6] and consists of three elements. The first element provides an overview of the purpose, state variables and scheduling of the model. The second element explains general concepts underlying model design, and the remaining element provides details. The structure of the ODD protocol implies that redundancy can occur between the main document and the supporting information. The model was developed using CORMAS software (http://cormas.cirad.fr/en/outil/outil.htm).

2.1 Overview

2.1.1. Purpose

The model is a combined cellular automaton (CA) (SimPolilla, see Fig. S1 and [7]) and agent-based model (ABM) designed to explore the consequences of farmer's agricultural practices on insect pest infestation levels during an IPM extension program. In this paper, the model was used in the specific scope of exploring the role of cooperative behaviours among small-scale farmers to manage an invasive potato tuber moth *Tecia solanivora*, Povolny (Lepidoptera: Gelechiidae) in the Ecuadorian Andes. The model simulates information diffusion, cooperation cost and effect, system sustainability (pest control) and was used to explore effective strategies to increase food security in the Andean region.

2.1.2. State variables and scales

The model comprises two hierarchical levels: the environment and the agents. The environment incorporates the thermal characteristics of the agricultural landscape and the population dynamics of the pest (Fig. 1 of the main document). It is modeled through a CA of 6 per 6 cells. Each cell of the CA represents a 500 per 500 m area, the total area corresponding to the size of a community (as defined below). Elemental cells do not represent

individual potato fields but a territory, managed by single a group of farmers, in which the pest evolves. The spatio-temporal dynamics of *T. solanivora* (the pest) was driven by local environmental temperature and agents' actions. Pest infestation level was simulated in each cell of the CA.

The agents' level is represented by groups of potato growers. Various groups compose a community, *i.e.* groups of people living in the same locality and sharing common interests. A community is a clearly defined territory commonly referred as a village. In the Northern Andes, communities represent also a social and juridical network among people sharing the territory. In our model, each community contains 36 cells so that the total area is 900 ha, within the range of community sizes reported in central Ecuador [8]. In each community, we randomly placed 6 agents each one provided with a fixed land of 6 cells (Fig. 1). One agent represents a group of about 4 to 5 families of potato growers characterized by the same action taking rules and IPM knowledge, therefore applying similar agricultural practices in their fields. This is a common feature of the social organization in agricultural landscapes of the Ecuadorian Andes [9, 10]. If we assume that each family comprises 8 people, the density of inhabitants in our model is about 30 hab/km^2, in the range of population densities found in the study region (Municipal Government of Guaranda, Bolivar, Ecuador). Each land corresponds to the territory an agent manages, and either represents his own land or one attributed to him by the community.

In our model, cooperation among agents occurred through the diffusion of IPM information from a trained agent through a FFS (named "graduate agent") to other agents (named "exposed agents") [11]. Agents were characterized by the following state variables: 1) their location within their community, 2) their IPM knowledge, 3) the number of actions (related to potato farming) they can do during one model step (named 'time credits' in the rest of the text), 4) their level of cooperation with other agents and 5) their social network (communication range) (Table S1).

We initiated model simulations with one graduate agent trained during a FFS and then simulated information diffusion through the community. Other agents had a IPM knowledge based on an empirical survey from farmer communities (see section 2. Empirical data). We defined a level of cooperation as the variable driving the willingness to diffuse of information through the community. Information diffusion occurred only on a fixed range of cells defined by the communication range state variable. As agents represent groups of farmers, this state variable introduces randomness in the probability of occurrence of a training session between two agents. All the parameters used in the model are summarized in Table 1. Each time step in the ABM corresponded to one pest generation (about two months).

2.1.3. Process overview and scheduling

The pest infestation level in each cell was driven by a CA (SimPolilla), whose conceptual description of processes and scheduling is provided in [7]. Briefly, it models the spatial temporal dynamics of the tuber moth *T. solanivora* in the Andes. Survival and reproduction are temperature dependent and dispersion through the landscape occurs through density-dependent diffusion.

Depending on their state variables values and pest infestation level in their field, each agent can make choices among alternatives behaviors with an associated cost in terms of time credits: 1) to be trained by a graduate agent about IPM practices, 2) to train an exposed agent about IPM practices, 3) to control the pest. Agents move randomly within their land after each action performed. Time is modeled as discrete steps and state variables are updated at each agent's action within a time step.

2.2. Design concepts

2.2.1. Emergence

Pest infestation level included density-dependent dispersion and temperature-dependent survival and fecundity. Pest infestation level was also influenced by agents through IPM-knowledge based control so that pest population dynamics emerges from both the CA variables and agents' behavior.

2.2.2. Adaptation

Agents make decisions depending on their IPM knowledge, their pest infestation level, their social network (other agents in their communication range), their remaining time credits, and their level of cooperation.

2.2.3 Objective

Agents' main objective is to decrease pest infestation level on their land, thereby implicitly increasing their crop production and incomes.

2.2.4. Learning

As agents learn from others, they increase their IPM knowledge and pest control at two levels: 1) in their own fields and 2) in the whole community as they can train other agents to better control pest on their land.

2.2.5. Prediction

The tacit prediction of our model is that by training exposed agents, graduate agents would reduce pest infestation events from neighboring lands, therefore meeting their main objective.

2.2.6. Sensing

Agents perceive pest infestation level on their land. They also perceive both location and IPM knowledge of other agents in the community. We assumed that an agent A_1 can perceive the IPM knowledge of an agent A_2 thanks to observation of the level of pest infestation on A_2's land.

2.2.7. Interaction

Within a community, agents interact directly through informal IPM training sessions. Interactions are local, *i.e.* within the same community and within a range of 5 cells between agents (see hereafter for a discussion on communication range).

2.2.8. Stochastic factors

Stochastic factors are included in two sub-models. First, potato moth population dynamics is driven by stochastic temperatures within the range of those observed in the region [12]. Second, agents move stochastically within their land. Random numbers are generated using the VisualWorks #Random function (VisualWorks 7.5 Cincom Systems). Sensitivity analyses based on 100 replications over 120 time steps allowed us to analyze the outcome of the multiple sources of stochasticity resulting from the combination of our different sub-models.

2.2.9. Observation

Two types of data were collected from our model: IPM knowledge of agents and pest infestation levels. These data were collected at each time step and stored into external files.

2.3. Details

2.3.1. Initialization

a. Level of pest infestation

The initial level of pest in the grid cell was fixed to 1, the carrying capacity.

b. Agent location

Agents were randomly located on one of the 6 cells composing their land.

c. *IPM knowledge*

Following [13], we define knowledge as "*the possession of analytical skills, critical thinking, ability to make better decisions, familiarity with specific agricultural practices, and understanding of interactions within the agro-ecological system*". Here, we focus on agent knowledge regarding IPM, and particularly potato moth control (see [14] for details on potato moth control practices).

To set up the IPM knowledge X_a of each agent in the community, we used empirical data obtained from through interviews (see Appendix S1) during field surveys. As most IPM knowledge and practices for potato moth control are relatively easy to understand (*e.g.*, keep the storage clean, store tuber in appropriate sacks), farmers can potentially answer correctly to all items of the interviews. Note, however, that there is often a limitation in the application of this knowledge, leading to limitation in IPM practices. This is actually shown by our survey of IPM knowledge levels within farmer communities (Fig. 2C) where no farmers with IPM knowledge = 5 were found. However, after an IPM session through farmer field school, we did observe that the level of knowledge can increase up to 5 (Fig. 2B). Based on these field data, we considered that the baseline proportion of the IPM knowledge scores (0, 1, 2, 3, 4, and 5) among agents was 1/6, 1/3, 1/3, 1/6, 0, and 0, respectively (Fig. 2A). We then simulated a scenario of IPM information spread where one agent has been trained through a FFS (IPM knowledge set to 5, see Fig. 2B) and potentially train the other agents in the community. The initial location of the graduate agent did not influence the model outputs for both IPM knowledge and pest infestation (see sensibility analysis performed by testing each potential location with 100 repetitions per location, Fig. S2).

d. Communication range

Fixing the value of communication range among agents was difficult due to the lack of empirical data. Consequently, we performed a sensitivity analysis to examine how communication range among agents, ψ, would influence pest infestation level dynamics in the community (Fig. S3). Results showed that for $\psi > 3$ (*i.e.* 1.5 km) the dynamics of pest infestation was not affected. Field observations and discussions with farmers revealed that farmers commonly communicate and cooperate with farmers living to distances greater than 1.5 km. The communication range among agents was set to $\psi = 5$ cells. As mentioned above, agents represent groups of farmers so that communication range introduces randomness in the probability of occurrence of a teaching session between two agents.

e. *Actions and time credits*

In our model, agents can perform two types of actions related to potato farming: 1) to conduct pest control applications (whose efficiency depends on their IPM knowledge) and 2) to exchange IPM information (either by being trained or training) so that they can increase their own IPM knowledge or that of other agents. These actions require time so that we included in our model two time credits parameters, $\theta_{training}$ and $\theta_{control}$, for each type of action. We assumed that the total time θ_{total} farmers dedicate to potato farming was:

$$\theta_{total} = \sum(\theta_{training} + \theta_{control}) \quad \text{Eq. 1}$$

To define the different θ values we first arbitrarily set up $\theta_{total} = 5$ for each time step of the model. Then, following [3], who proposed that Andean farmers would accept to dedicate up to 10% of their total time (*i.e.* about 40% of their potato growing time) to IPM training sessions, we fixed $\theta_{training} = 2$. Finally, because IPM training is a time consuming process [13], we assumed (by default) that twice more time was needed to train than to control and fixed $\theta_{control} = 1$. The three potential combinations to use 5 units were: 1) 5 pest control actions, 2) 3 pest control actions + 1 training action, 3) 2 training actions and 1 pest control action. As one time step corresponds to 5 credits agents can do both training and pest control in each time step.

We performed a sensitivity analysis to explore how $\theta_{training}$ values would influence pest infestation level dynamics (Fig. S4). The dynamics of pest infestation levels was similar among the four simulations, except in a short time frame between 4 and 7 years where infestation levels were slightly higher for lower $\theta_{training}$ (maximum 10% after 5 years).

2.3.2. Input data

The stochastic factor used to modify temperature in each cell of the model was based on temperature variations measured in the study region (see the data in appendix 1 in [12]). Our model does not use other input data to represent time-varying processes.

2.3.3. Sub-models

a. Potato moth population dynamics

Details concerning this sub-model are described in SimPolilla (see [7] for a full description, validation, and sensitivity analyses).

b. Potato moth control by agents

Our field survey revealed that potato moth control increased linearly with increasing IPM knowledge of farmers ($R^2 = 0.51$, intercept $d = 0.21$, and slope $c = 0.15$; $P < 0.001$; see Fig 2C in the main document). Consequently, in our model, moth control Δ_i by an agent a with an IPM knowledge X_a was calculated as follows:

$$\Delta_i = cX_a + d + \sigma \quad \text{Eq. 2}$$

With σ the variance of pest control for a given IPM knowledge score given by box-plots in Fig. 2C in the main document.

c. IPM information diffusion

In our model, the decision of agents whether or not to share information (and their consequence on pest infestation levels) is included at three different levels. First, agent's decision is explicitly calculated as a function of the level of pest infestation in their own fields, itself dependent on their IPM level of knowledge. As evidence by our field surveys, IPM level of knowledge level is closely related to farmer's financial resources and personal situation within the community (see Dangles *et al.* 2010). Second, IPM diffusion process followed rules obtained from real-world data on the extent and the efficiency with which farmers share their knowledge (see Fig. 2B). We were indeed aware that many factors, including the social and economic status of farmers, may influence their decisions. However, obtaining reliable field data allowing establishing direct relationships between these factors

and farmers' IPM behavior is a challenging issue which has long been recognized by IPM extension program worldwide [25]. We therefore assumed that the real-world data of knowledge sharing included in our model represented the outcome of a decision making process made by farmers, including all sorts of important factors generally included in ABM such as information about incentives, payoffs, constraints such as economic cost, and uncertainty about the outcome. For example, if a farmer share the information with only 1 neighboring farmer, this could be due to various reasons such as 1) he has no incentive to share it (no problem with pest control), 2) he has a low social position in the community, or 3) limited financial resources make him dedicating his time to activities resulting in direct economical benefits (*e.g.*, crop management, market). Third, we used our ABM to explore the relative benefits of IPM information sharing for pest control by explicitly comparing outcomes of simulations based on real-world diffusion process *vs.* a theoretical situation in which agents would not share information at all (see Fig. 5).

Technically, IPM information diffusion between two agents could occurred if the following conditions were fulfilled: 1) both agents should have different IPM knowledge (the agent with higher knowledge trained the other agent), 2) both agent should be located within a range of $\psi = 5$ cells from each other (communication range), and 3) both agents should have the necessary time credits left for a training IPM session ($\theta_{total} \geq \theta_{training}$). Agents preferentially assist neighbors, since this will increase their own potential pest protection. We considered that the efficiency of information diffusion was constant whatever the IPM knowledge scores of both graduate and exposed agents.

d. Agents' movement

Agents moved randomly within their land after each action performed.

3. Model analysis: verification and validation

3.1. Verification

All sub-model of our ABM were tested using an external programming language [15] so that we verified that 1) the model was programmed correctly, 2) the algorithms were implemented properly, and 3) the model did not contain errors, oversights, or bugs. In addition to such routine verification, we also made verification that our model correctly reflects the workings of real-world process. In our case, one of the most important processes to reproduce was the relationship between IPM knowledge of farmers and pest control (see field data on Fig 2A of the main document). We did find that our model correctly reflected the relationships between IPM knowledge and pest control provided by field data (Fig. S5). No significant differences were found between the two regressions (ANCOVA, $F = 0.97$, $P = 0.654$).

3.2. Validation

The process of how new products or innovations get adopted as the consequence of interactions between users and potential users is traditionally modelled using the Bass model [16]. This model has been widely used in marketing and management science [17, 18]. Because this model fits the data of almost all product introductions, we used it to validate our agent-based diffusion of information, ensuring that our model correctly reproduces observed patterns in the literature. One interpretation of the Bass model was that the time *t* from information training until adoption is assumed to have a probability distribution *N(t*), which can e expressed as follows:

$$N_{t+1} = N_t + p(m - N_t) + qN_t(m - N_t) / m \qquad \text{Eq. 3}$$

where *p* represents the coefficient of external influence, *q* the coefficient of internal influence and *m* the number of trained agents.
Eq. 3 is a difference equation and its solution is:

$$N_t = m * (1 - e^{-(p+q)t}) / (1 + (q/p)e^{-(p+q)t}) \quad \text{Eq. 4}$$

Bass curve fitting to our ABM output data and estimation of *p*, and *q*, were performed following [19] and [20].

3.3. Analysis of the influence of cooperation

Although recent studies have shown that humans can behave altruistically [21, 22], decision of poor farmers to cooperate in a context of crop protection is likely to be driven by self interest (in fact, survival) rather than altruism [23]. In addition, farmers are more likely to behave depending on problems they physically perceive on their land rather than on behalf of agenda set by externally based science and development initiatives [2]. For those reasons, we assumed that farmers would be more prone to cooperate in IPM information diffusion when they perceived that a pest represents a danger for their crop production. Consequently, varying levels of cooperation in our model were obtained by changing the "pest danger threshold" perceived by agents, that is to say the pest infestation level that triggers a control action: lower threshold levels generated higher cooperation levels among agents (increased frequency in training session) and vice versa. This allowed us to fully couple both social and pest dynamics sub-models in our assessment of the role of cooperation for the success of IPM programs. Results of this analysis are presented in the Fig. 5 of the main document.

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Figure and table legends

Fig. S1. Simplified representation of the pest model.

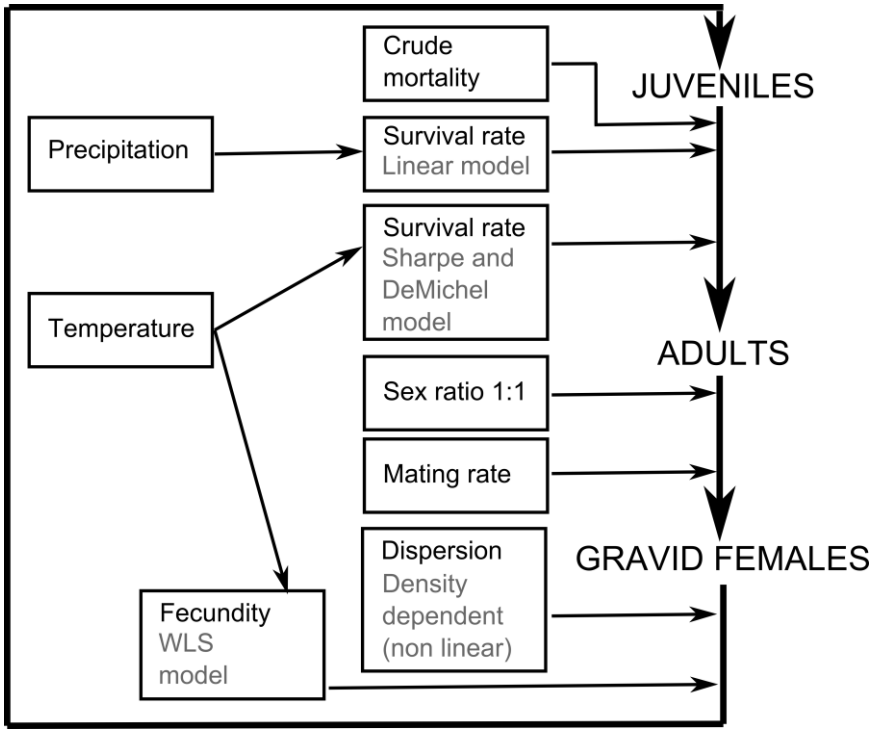
Fig. S2. Effect of initial spatial configuration on information diffusion. Each plot A, B, C, D, E and F are located in the figure to match the model configuration. Each curve represents the average IPM knowledge of 100 simulations for one agent, with standard deviation in dots. The red curves represent the information diffusion when initial graduate agent is in position C (central) and the black curves when he is on position A (corner), showing no significant difference in the information diffusion process.

Fig. S3. Sensitivity of pest infestation levels to variations in the communication range parameter ψ (from 1 to 10 cells). Curves are the mean of 100 simulations during 120 pest generations (20 years).

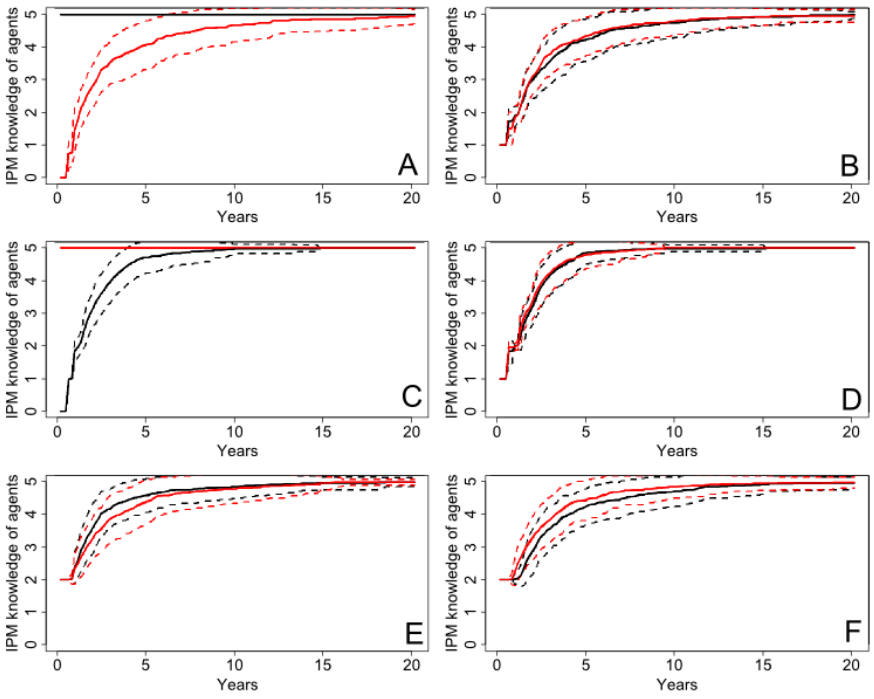
Fig. S4. Sensitivity of pest infestation levels at the community level (6 agents) to variations in the time credit parameter. Figure S4A represents variations in training time credit parameter $\theta_{training}$ (from 1 to 4 credits) and figure S4B variations in control time credit parameter $\theta_{control}$ (from 1 to 5 credits). Simulations with $\theta_{training} = 5$ were omitted as no farmer would spend 100% of his time in training sessions. Curves are the mean of 100 simulations during 120 pest generations (20 years).

Fig. S5. **Comparison of the relationship between IPM knowledge and pest control** either using data observed (in dark grey) or data simulated by our ABM model (in light grey). Thin lines represent the 95% confidence intervals.

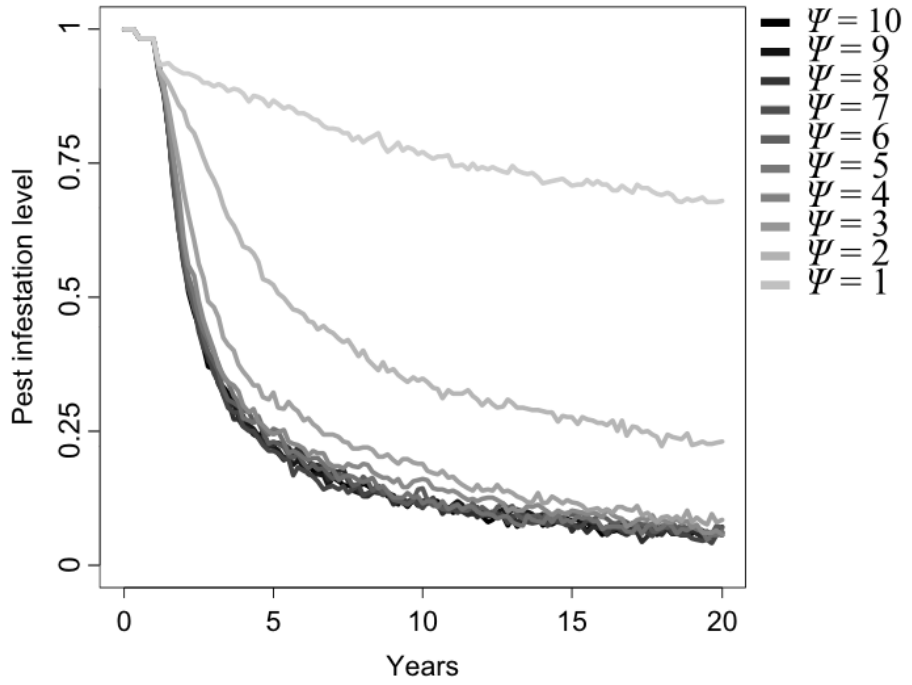
Table S1. **Model parameters**. *a* and *i* denote parameters related to agents and cells, respectively.


Crude mortality
JUVENILES
Precipitation
Survival rate Linear model
Survival rate Sharpe and DeMichel model
Temperature
ADULTS
Sex ratio 1:1
Mating rate
Dispersion Density dependent (non linear)
GRAVID FEMALES
Fecundity WLS model

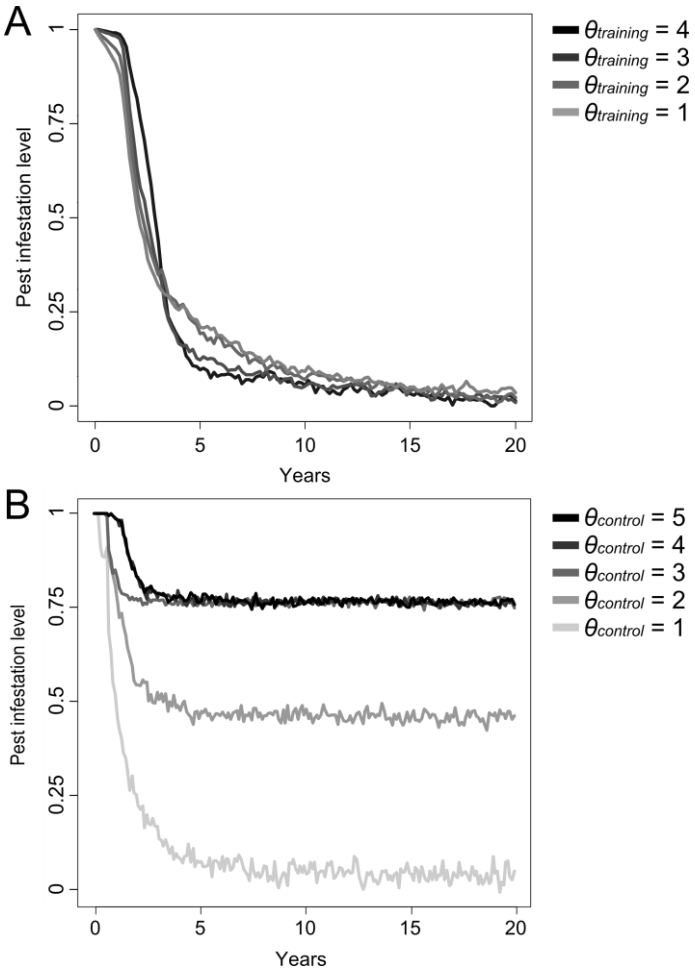
S1


IPM knowledge of agents
Years
A
B
C
D
E
F

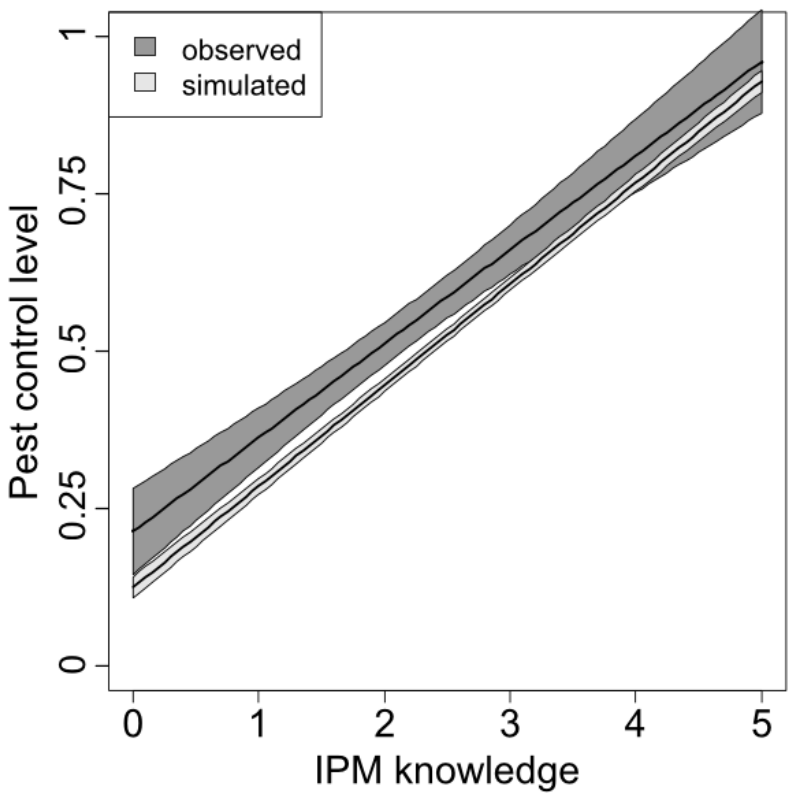
S2


Pest infestation level
0
0.25
0.5
0.75
1
0
5
10
15
20
Years
Ψ = 10
Ψ = 9
Ψ = 8
Ψ = 7
Ψ = 6
Ψ = 5
Ψ = 4
Ψ = 3
Ψ = 2
Ψ = 1

S3


A
Pest infestation level
0
0.25
0.5
0.75
1
0
5
10
15
20
Years
θtraining = 4
θtraining = 3
θtraining = 2
θtraining = 1
B
Pest infestation level
0
0.25
0.5
0.75
1
0
5
10
15
20
Years
θcontrol = 5
θcontrol = 4
θcontrol = 3
θcontrol = 2
θcontrol = 1

S4



S5

Parameters	Name	Unit scale	Type
IPM knowledge	X_a	[0:5]	Field data
Moth control (auxiliary variable)	Δ_i	[0:1]	Field data
Information diffusion efficiency	E	[0:1]	Field data
Pest infestation level	G_i	[0:1]	CA output
Level of cooperation	K_a	[0:1]	Variable
Time credits	θ_a	5	Constant
Communication range	Ψ	5	Constant

Table S1

Questionnaire (in Spanish) use to measure the knowledge of farmers concerning the IPM of potato moths in Ecuador

☐ Hombre ☐ Mujer Edad**: _ _ _ _ _ _ _ _ _ _ _ _** Comunidad: _ _ _ _ _ _ _ _ _ __

1. ¿Conoce acerca de la Mariposa de la papa?
☐ Si ☐ No

2. ¿Como cree que llegó la polilla de la papa a su campo?
☐ Dentro de la semilla ☐ Volando ☐ Caminando ☐ Otras ……..

3. Cuantos tipos de polilla de la papa conoce? …….

4. Podría describir como son la/as polillas o mariposas de la papa que conoce?
☐ Con círculos en las alas ☐ Con triángulos en las alas ☐ Puntitos en las alas ☐ Otras……

5. Conoce cómo se reproduce la polilla de la papa? Explique
☐ No ☐ Si……...

6. Describa los cambios que sufre la polilla de la papa durante su vida?
☐ Huevo, larva o gusano, adulto o mariposa
☐ Huevo, larva o gusano, pupa o adivinador, adulto o mariposa
☐ Larva o gusano, adulto o mariposa
☐ Otra.....

7. En que estado de la vida de la polilla produce daños al tubérculo?
☐ Huevo ☐ Larva o gusano ☐ Pupa o adivinador ☐ Adulto o mariposa ☐

8. ¿Conoce usted a que parte de la planta de papa ataca la polilla?
☐ Hojas ☐ Tallo ☐ Tubérculo

9. ¿En que parte o lugar a visto a los adultos o mariposas de la polilla de la papa?
☐ Base de las plantas ☐ Hojas ☐ Bodega

10. ¿Según Usted en que condiciones climáticas aumenta más la polilla?
☐ Calor ☐ Frío ☐ Lluvia ☐ Viento

11. ¿Se puede sembrar la semilla si esta picada?
☐ Si ☐ A veces ☐ Trato de no hacerlo ☐ Nunca

12. ¿Que rotación de cultivos usted hace?
☐ No roto ☐ Papa / pasto ☐ Papa / otros cultivos: _ _ _ _ _ _ _ _

13. Después de haber preparado el suelo:
☐ Siembro inmediatamente para ganar tiempo
☐ Dejo pasar unos días: ¿cuantos días? _ _ _ _ _ _ _ _ _ _ _ _

14. ¿Usted hace aporque en su cultivo de papa?

☐ No
☐ Si: ☐ Aporque normal ☐ Aporque alto

15. ¿Una vez que las plantas han madurado, usted corta el follaje?
☐ No, dejo que se marchite en el campo ☐ A veces
☐ Si: ¿Que hace con este follaje?
☐ Lo dejo en el cultivo ☐ Lo boto en una quebrada ☐ Lo quemo
☐ Lo utilizo como comida para el ganado

16. ¿En el caso que tenga papa picada o poco picada, que usted hace?
☐ La dejo en el cultivo ☐ La doy a los chanchos
☐ La boto en una quebrada ☐ La entierro profundo

17. ¿Cómo usted guarda la papa cosechada?
☐ Amontonada
☐ En sacos: ☐ normales ☐ ralos

18. ¿Usted realiza limpieza del almacén antes de guardar las papas?
☐ No ☐ Si ☐ A veces

19. ¿Usted fumiga el almacén?
☐ No ☐ Si ☐ A veces

20. ¿Usted utiliza plantas como Eucalipto o Marco como repelentes?
☐ No ☐ Si ☐ A veces

5. Modélisation multi-agents de la dispersion induite par l'homme d'espèces envahissantes dans le paysage agricole (Appendix)

Appendix 1: Description of the cellular automaton used to simulate the pest using the ODD protocol

The model description follows the ODD protocol for describing individual- and agent-based models (Polhill *et al.* 2008; Grimm *et al.* 2006; Grimm & Railsback 2005) and cellular automaton (Grimm *et al.* 2006, appendix A p136-147). Note that in the case of cellular automaton, some of the design concepts of the ODD protocol do not apply. The model was developed using CORMAS (CIRAD, France, http://cormas.cirad.fr) based on the VisualWorks programming environment (CincomSmalltalk, http://www.cincomsmalltalk.com).

OVERVIEW

Purpose

The SimPolilla model was developed to describe the invasion and diffusion of the potato tuber moths (PTM) (*Tecia solanivora*, *Phthorimaea operculella and Symmetrischema tangolias*, Gelechiidae, Lepidoptera), tiny moths that invaded the agricultural landscape of the North Andean region in the last decades. The larvae of these moths are serious pests of potatoes, one of the main food crops of the region. A second objective of the model was to make prediction and generate maps of invasion risk for local farmer communities. The model was developed and validated in a pilot region of central Ecuador but was built to be applicable to a much wider geographic range in North Andes.

State variables and scales

The model is based on biological and ecological rules derived from field and laboratory experimental data for the three PTM species (Dangles & Carpio 2008; Dangles *et al.* 2008; Roux & Baumgärtner 1997). The Simiatug valley, used as a pilot region to build the model, is located in the province of Bolívar, in the central highlands of Ecuador. We focused on a study area of 40 x 40 km represented by a grid of 6,400 cells with a cell size of 0.25 km². Each cell *i* is characterized by its quality of habitat n_i *i.e.* the quantity of food resources available for the moth larvae. We consider that n_i was fixed to 0 or 1 depending on the land use (ie. crops or other uses such as woods or highlands). Each cell is also characterized by a range of temperature values (mean $T_{moy\ i}$, maximum $T_{max\ i}$ and minimum $T_{min\ i}$ in ºC), a monthly amount of precipitation $P_{i;j}$ (in mm), and a mean elevation α_i (m.a.s.l.).

Table 1. Full set of state variables in SimPolilla

	Name of variable		Units
Habitat	Quality of habitat of cell i	n_i	
Temperature	Average mean temperature over 30 years per cell i	$T_{moy\ i}$	ºC
	Average minimum temperature over 30 years per cell i	$T_{min\ i}$	ºC
	Average maximum temperature over 30 years per cell i	$T_{max\ i}$	ºC
Precipitation	Average precipitation amount over 30 years per cell i and per month j	$P_{i;j}$	mm
Elevation	Elevation on the study zone per cell i	α_i	m

PTM species	Level of infestation of juveniles density of specie k per cell i (k = 1, 2 , 3; *T. solanivora, P. operculella, S. tangolias*, respectively)	$J_{k;i}$	Number
	Level of infestation of adults density of specie k per cell i (k = 1, 2 , 3; *T. solanivora, P. operculella, S. tangolias*, respectively)	$A_{k;i}$	Number
	Level of infestation of gravid females density of specie k per cell i (k = 1, 2 , 3; *T. solanivora, P. operculella, S. tangolias*, respectively)	$G_{k;i}$	Number
Distance covered by a moth	Distance covered by a moth	d	Meters

The higher-level entities are based on the number of gravid females of the three PTM species. Each time step represents one PTM generation based on *T. solanivora* life cycle duration (*i.e.* about 3 months at 15°C). An adjustment is made on the two other species so that each step corresponds to one PTM generation. The 500 × 500 m scale for cells was chosen for fitting the level of precision we have concerning PTM dispersion, based on available knowledge on moth dispersion (Cameron *et al.* 2002 [B]). Temperatures, precipitations and elevations have a 1 per 1 km resolution. Inside a square of four cells, these parameters have the same value.

Process overview and scheduling

In this section, we briefly describe the processes and scheduling of our model. Details are given in the submodels section. Each process is presented according to its sequence proceeding and in the order at which state variables are updated. Each time step is one *T. solanivora* generation.

Table 2. Processes of SimPolilla model

Process	**Submodels**
State variables update	State variables update
Stochastic temperature	Stochastic temperature
Stochastic rainfall	Stochastic rainfall
PTM mortality	Crude mortality Temperature dependent mortality Precipitation dependent mortality
PTM dispersal	Neighbourhood dispersal
PTM reproduction	Mating rate Sex ratio Temperature dependent fecundity

Process: state variables update

Each state variable corresponding to real data (Almanaque Electrónico de Ecuador by Alianza Jatun Sacha – CDC, digitised by DINAREN, 2003 ; Hijmans *et al.*, 2005), is imported from individual files (one per layer), so that SimPolilla may be easily adapted to other regions.

Process: stochastic temperature

Mean temperature is transformed according to a stochastic factor (Box & Muller 1958).

Process: stochastic rainfall
Two consecutive monthly precipitations are randomly chosen during a given step.

Process: PTM mortality
PTM population is updated according to crude, temperature and precipitation mortality.

Process: PTM dispersal
PTM disperse through the territory from one cell to another by diffusion.

Process: PTM reproduction
PTM populations are updated according to biological rules (mating rate, sex ratio, fecundity). A correction is made over fitness on the two other PTM species to adjust time step based on *T. solanivora* life cycle.

DESIGN CONCEPTS

In Simpolilla model, moths' implicit objective is to infest the considered landscape by maximizing dispersal speed. Emergent key results are level of infestation in each cell and infestation speed. Interspecific interactions are not taken into account in this model and a stochastic factor over temperature and rainfalls are included mimic actual climatic variation.

DETAILS

Initialization and input

The environment is based on the Simiatug agricultural region (Bolivar, central part of Ecuadorian Andes), with temperature, precipitation and elevation from available data with a 1 km^2 resolution (Hijmans *et al.* 2005). Quality of habitat is based on GIS information about land use with a 0.25 km^2 resolution (Almanaque Electrónico de Ecuador by Alianza Jatun Sacha – CDC, digitised by DINAREN, 2003). The cellular automaton is a 4-connex square shaped grid, with closed boundaries as we are considering an existing geographical location. At the beginning of each simulation, PTM inoculums are placed in the Simiatug village and spread is observed and recorded for each species.

Submodels

In this section we describe the submodels given in table 2.

Climatic driver of PTM dynamic

Temperature

In order to feed the model with real climate variables, we chose to introduce a stochastic factor $T_{stochastic}$ in the model (see also Sikder *et al.* 2006) that allowed us to obtain by multiplication a stochastic temperature in cell i $T_{Sto\ i}$.

We use the polar form of the Box-Muller transformation (Box & Muller 1958), to generate a Gaussian random number, based on climatic data from the region (see Dangles *et al.* 2008 – appendix A). Random number used is based on random procedure in VisualWoks (VisualWorks® NonCommercial, 7.5 of April 16, 2007. Copyright © 1999-2007 Cincom Systems, Inc. All Rights Reserved.).

$$T_{Stochastic} = \sqrt{\left(-2 * \ln\left(x_1^{\,2} + x_2^{\,2}\right)\right)/ w} * \left(2 * random - 1\right)$$

(1)

$$with - \begin{pmatrix} random \in [0:1] \\ x_1 = 2 * random - 1 \\ x_2 = 2 * random - 1 \\ w = x_1^{\,2} + x_2^{\,2} \end{pmatrix}$$

The stochastic temperature replaces average temperature in all equations bellow.

Precipitation

As for temperature, we choose to introduce a stochastic factor to obtain a stochastic precipitation P_{Stoi}. Using a random number *j* from 1 to 12 (VisualWorks® NonCommercial, 7.5 of April 16, 2007. Copyright © 1999-2007 Cincom Systems, Inc. All Rights Reserved.), we take the average of the monthly amount of precipitation $P_{i;j}$ corresponding to the random number and the following.

(2) $$P_{Stoi} = \left(P_{i;j} + P_{i;j+1}\right)/ 2$$

PTM life dynamics

Data on development and survival for immature stages (eggs, larva, and pupa) and on fecundity for adults were acquired from two sources. First we used published data from laboratory experiments performed in the Andean region (Notz et al 1995; Dangles *et al.* 2008). Second we used data obtained within the last 8 years at the Entomology Laboratory at the PUCE (Pollet, Barragan & Padilla, unpublished data). For these two sources, only data acquired under constant temperatures (± 2°C) were considered. In all studies, relative humidity ranged from 60 to 90%, values above any physiological stress.

Crude mortality

Overall force of mortality among a population is the sum of crude cause-specific forces. Here we consider innate mortality (λi), dispersal related mortality (λd) and predation (λe) (see Roux, 1993; Roux et al, 1997) for *P. operculella*.

(3) $$S_{i,d,e}(x) = e^{-(\lambda i + \lambda d + \lambda e)*x}$$

Innate mortality is not taken into account using equation (3), because a temperature dependent parameter fits better to reality than λi (see bellow).

We are also considering separately survival rate with predation $S_{Predation}$ by birds, spiders, ants and others predators for the adult stage following equation (4) (Tanhuanpää *et al.* 2003). Level of predation σ_i scales from 0 to 10 (ie 10 the lower, 0 the higher level), in order to simulate different scenarios, from theory to reality.

(4) $$S_{Predation} = 1 - e^{\left(\frac{-\sigma_i}{20} * \sigma_i\right)}$$

Temperature dependent mortality

Temperature is the most basic controller in poikilothermic organisms (Zaslavski *et al.* 1988). Survival rate under laboratories conditions has been studied for the three PTM species, using a temperature dependent kinetic model.

We used the following equation to calculate the survival rate S_D for each stage at each temperature for which data were available:

(5) $$S_D = S_T^{\frac{1}{D_D}}$$

with S_T the total survival at the given stage, expressed as a proportion, and D_D the days to development.

Following Roux (1993), we applied the Sharpe and DeMichel model (eq. 5) to the survival-response to temperature as in equation 6:

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

with a, b, c, d, e, and f the equation parameters to be estimated.

Table 3. Parameter values of the kinetic model (equation 7) describing the stage specific survival rate $S_D(T)$ response of the three invasive PTM species (*T. solanivora*, *P. operculella*, and *S. tangolias*) to constant temperatures. Note that temperature is given in Kelvin degrees.

Species	Instar	a	b	c	d	e	f
S. tangolias	Egg	0,834	10,94	-234000	282,4	616600	304,1
	Larva	0,694	-236,3	-420300	283.1	1551000	305,6
	Pupa	0,882	39,93	-992700	282,9	1110000	304,7
P. operculella	Egg	0,917	50	-200000	283.3	400000	310.1
	Larva	0,950	-150	-400000	284.4	900000	310.0
	Pupa	0,960	50	-800000	283.1	700000	312.2
T. solanivora	Egg	0,822	-758,5	-212100	281,9	405200	303,8
	Larva	0,758	-180,2	-475700	282,7	1298000	301,5
	Pupa	0,900	-73,72	-1263000	286,5	1095000	306,3

For temperatures higher than 13°C, *P. operculella* immature stages showed higher survival rates (0.9-1.0) and tolerance to high temperatures (up to 37°C) than the two other species. Both *T. solanivora* and *S. tangolias* had a slightly better tolerance to low temperatures than *P. operculella*.

Precipitation dependent mortality

Precipitations play a minor but significant role in moth survival rate (Wakisaka *et al.* 1989; Kobori *et al.* 2003). Because each insect stage is concerned and because no studies have been conduced on PTM, we use a correcting factor on survival rate. This rate is dependent on the amount of precipitations in mm over two months randomly chosen on the GIS database (SICAGRO). The correcting factor is adjusted from hypothetical relationship based upon available knowledge.

Neighborhood dispersal

We consider that the fraction of PTM leaving a cell is dependent on adult population density and quality of habitat n_i within the cell (see also Bendor *et al.* 2006 [A; B]; Eizaguirre *et al.* 2004). PTM do not have a perception of the environment situated in a neighborhood cell. According to Bendor *et al.*, we assume that emigration rate (ye), follows an s-shaped curve, which levels out as it approaches the maximum density (carrying capacity). Density is a fraction of K, carrying capacity (0 < density < K).

$$(7) \qquad ye = \frac{0.4}{\left(1 + 0.1 * e^{\left(-0.005 * \left(A_{k;i} - (K-200)\right)\right)}\right)} * \left(1 - n_i\right)$$

We assumed that PTM can travel up to 200 m away from their origin during a generation (larvae can hardly move to 1 m and adults life time is very short). The probability of a PTM to cover a defined distance (yd) is a decreasing function of emigration rate. This function may certainly overestimate PTM dispersal but we prefer overestimation than below estimation (Cameron *et al.*, 2002 [A; B]).

$$(8) \qquad yd = e^{\left(-0.015 * distance\right)}$$

As our unit cell is 0.25 km^2, each migrating PTM, depending on its position on the square, and on distance covered d, has a probability (yeR) of crossing the cell boarder. We assume that PTM move inside the cell either horizontally or vertically. This assumption may certainly overestimate PTM dispersal but we prefer overestimation than below estimation (Cameron *et al.* 2002 [A; B]).

$$(9) \qquad yeR = \frac{\left(cellSurface - \left(longCell - 2 * d\right)^2\right)}{cellSurface}$$

Reproduction

Mating rate

Mating rate is correlated with age, sex ratio and weigh of individuals, but also with distance from one individual to another (Makee *et al.* 2001; Cameron 2004). No specific studies have been made on mating rate under natural conditions, and laboratory measurements may frequently represent an overestimation of the natural situation because laboratory females have little opportunity to avoid mating (Reinhardt 2007). However, as our cells are 500 m long, and thanks to field observation, we know that pheromones works at least on a 200 m radius, and we assume that within a cell, mating rate is equal to one no matter the density.

Sex ratio

Among PTM population, sex ratio has been studied and is 1:1 (Saour 1999). After dispersal, the remaining adult population, combined with the mating rate and the sex ratio give the gravid females population.

PTM fecundity

Although energy-partitioning models have been developed to explain the shape of insect fecundity as a function of aging (Kindlmann *et al.* 2001), we are not aware of any mechanistic models that describes insect fecundity as a function of temperature. Several probabilistic non-linear models to fit insect fecundity across temperature have been proposed in the literature (Roux 1993; Lactin *et al.* 1995; Kim et Lee 2003; Bonato *et al.* 2007), but none of them gave us significant results with our data ($r < 0.35$, $F_{stat} < 2.01$). We therefore used weighted least square (WLS) regression to find the best model that fits our fecundity data across temperature. WLS regression is particularly efficient to handle regression situations in which the data points are of varying quality, *i.e.* the standard deviation of the random errors in the data may be not constant across all levels of the explanatory variables, which could be the case. For the three tuber moth species, the best fit was obtained with the

Weibull distribution function, which has long been recognized as useful function to model insect development (Wagner *et al.* 1984).

The effect of temperature upon fecundity was well described by the Weibull distribution functions (r^2 = 0.75, 0.83, and 0.91 for *T. solanivora*, *S. tangolias* and *P. operculella*, respectively). Results showed marked differences among PTM species, both in terms of total numbers of eggs laid per females and optimal fecundity temperature : the highest fecundity was found in *T. solanivora,* with about 300 eggs/female at 19°C, followed by *S. tangolias* (220 eggs/female at 15°C) and *P. operculella* (140 eggs at 23°C).

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Appendix 2: Animations

The following animations illustrate simulations in which blue and red figurines represents agents, and blue and red links agents' movements from 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 infested 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.

Figures available at jasss.soc.surrey.ac.uk/14/3/7.html part A5.1-4

Figure A-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.

Figure A-3. 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 from village to village.

Figure A-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.

6. Communiqués de presse

6.1. Mise en avant sur le site de PLoS (« Featured Research ») :

6.2. Communiqué de presse PLoS sur News Ecology :

6.3. Communiqué de presse PLoS sur EurekAlert! (AAAS) :

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Agricultural pest management program efficiency challenged by information diffusion barriers among farmers

While international pest management programs have long relied on farmer cooperation to spread pest control information at larger scales, a study by French researchers published in the open-access journal *PLoS Computational Biology* on Thursday 13th October 2011 reveals that slow information diffusion within farmer communities gives rise to significant lags in implementation of pest management procedures.

Food security of millions of people in the developing world has faced a growing number of challenges in recent years, including risks associated with emergent agricultural pests. While pest management programs have a larger place than ever on the international policy agenda, the debate concerning their efficiency at large scales has remained unresolved. Pest management practices that rely on farmer cooperation to share pest control information have been favoured, but the efficiency of such methodologies has been questioned due to incomplete knowledge of variation in farmers' practices, and their complex interactions with pest dynamics. A modeling framework, integrating both social and ecological perspectives, was therefore needed to better predict the efficiency of pest management programs.

The modeling framework developed by the authors was comprised of an agent-based model combining social (information diffusion theory) and biological (pest population dynamics) models to study the roles played by cooperation and sharing of pest management information among small-scale farmers in controlling an invasive pest. The model was implemented with field data from large-scale surveys of approximately 300 farmer households in the Ecuadorian Andes, and was undertaken within a regional pest management program funded by the French Institute for Research and Development (IRD) and the McKnight Foundation.

Though the slow learning process places restrictions on the knowledge that can be generated using cooperative pest management practices, the authors conclude that if individuals learn from others about the benefits of early prevention of pests, then a temporary educational effort may have a sustainable long-run impact on pest control.

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COMPETING INTERESTS: The authors have declared that no competing interests exist.

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6.4. Communiqué de presse PLoS sur FirstScience.com :

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Information Diffusion Key to Pest Management

OCTOBER 17, 2011 BY STEVEN FORREST LEAVE A COMMENT

A recent study has found that integrated pest management programs can experience significant lags in their implementation due to slow 'information diffusion' within farmer communities. Cooperation between farmers in developing countries was found to be key to ensure the successful coordinated implementation of such programs.

IPM tries to avoid dangerous pesticides. USAID Afghanistan

Integrated pest management (IPM) programs are biological approaches to dealing with invasive pests without using expensive and environmentally damaging pesticides. These can range from using pest traps, erecting insect barriers or introducing natural predators that prey only upon the pests and can fit into the ecosystem without any undesirable effects.

The study, published last week in *PLoS Computational Biology,* has found that these IPM programs are adversely affected by slow information diffusion within farming communities. In this case 'information diffusion' refers to the movement of knowledge from the scientists in charge of the project, to the individual farmers implementing this knowledge on their farms. The success of IPM programs depends on the fast information diffusion to farmers to allow a coordinated response to invasive pests. A coordinated response can eradicate an invasive pest, however a patchy response will leave small areas where the pest will still exist.

The researchers surveyed approximately 300 farmers in the Ecuadorian Andes who were part of a regional IPM program. They asked the farmers about their experiences in learning about the IPM program and their perspectives on teaching this to other farmers.

The trained farmers with a knowledge of the IPM program cited short term costs as an obstacle to information diffusion. They argued that by spending time training other farmers, who did not know how to implement the IPM program, they would experience an increase in pest infestation in their own land. However the researchers found that this cooperation paid off in the long term as it meant that there was a decreased pest infestation within the local community.

Information diffusion was found to be important in the coordinated implementation of IPM programs. The study suggests that future IPM programs in developing countries should include a short term educational effort that trains local farmers of the techniques needed and the benefits to themselves in training other local farmers.

Plantwise is aiming to make information available to farmers in two ways – face-to-face via a network of plant clinics in the developing world and internationally via a comprehensive global knowledge bank. This information includes distribution data, diagnostic tools and treatment advice using biological, cutural and chemical methods. We are working to alleviate the problems mentioned in the study above by encouraging fast information diffusion to farmers to allow a coordinated response to crop pests and diseases.

6.6. Communiqué de presse Sciences au Sud (Le journal de l'IRD - 59 - avril/mai 2011) :

Agriculteurs, ravageurs et jeu de rôles

Plus concret que *Donjons et Dragons* et plus utile que le *Monopoly*, les scientifiques développent un jeu de rôles pour former les agriculteurs équatoriens à la lutte contre de nouveaux ravageurs de la pomme de terre. L'enjeu est de sensibiliser les paysans des zones reculées au contrôle de ces insectes qui mettent en péril leur sécurité alimentaire. « *Les communautés andines ne disposent pas de savoirs traditionnels sur ces espèces invasives de papillons*[1]*, importées accidentellement du Pérou et du Guatemala il y a une quinzaine d'années,* explique l'écologue Olivier Dangles qui est à l'origine de cette initiative. *Elles sont donc très dépendantes d'interventions extérieures pour connaître et appliquer les mesures élémentaires de prévention.* »

La démarche des chercheurs vise à convaincre les cultivateurs les moins informés de surveiller l'évolution des populations de ravageurs dans leurs champs, grâce à des outils aisés à construire et à mettre en œuvre, afin d'intervenir rapidement en cas d'infestation. Elle leur présente également des méthodes simples de protection des cultures et met en scène l'intérêt à les appliquer.

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Sur un plateau de jeu représentant les terres de leur communauté, les paysans équatoriens apprennent les bonnes pratiques pour préserver leurs cultures d'insectes ravageurs invasifs.

Concrètement, il s'agit de réunir des groupes de paysans autour d'un plateau de jeu représentant les terres cultivées de leur communauté. Chaque case figure la parcelle d'un des participants. « *Nous leur posons des questions techniques sur leurs pratiques agricoles : qui nettoie son champ après la récolte, qui fait de la rotation des cultures, qui stocke sa production en sac, etc.,* raconte le chercheur. *À chaque étape, ils mettent une carte de couleur sur leur case, verte, bleue, jaune, orange ou rouge, selon que leur habitude est bonne ou moins bonne.* »

Les réponses sont ensuite entrées dans un modèle informatique multi-agents de la dynamique du ravageur, et les joueurs peuvent voir immédiatement l'impact de leurs actions, ou de leur inertie, sur l'infestation de leur parcelle et des parcelles contiguës. « *Pour ne stigmatiser personne et forcer le trait par l'exemple, nous dédions une case à un paysan virtuel qui ferait tout de travers,* précise-t-il. *Les autres voient ainsi clairement l'intérêt qu'il y a à adopter les pratiques culturales appropriées, pour soi, comme pour l'ensemble de la communauté.* »

Ce jeu devrait être largement utilisé par les services d'encadrement rural, qui sont coutumiers des approches participatives.Outil de formation des paysans, le jeu recèle aussi un volet recherches. Grâce aux réponses fournies par les joueurs, il permet d'alimenter les modèles multi-agents sur la dynamique des ravageurs, en données sur l'influence des comportements humains et sociaux.

Ces modèles informatiques sont également au centre d'un travail de thèse, mené au sein de l'équipe qui a développé le jeu de rôle par le modélisateur de systèmes complexes François Rebaudo.

1. Des teignes de la pomme de terre.

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6.7. Communiqué de presse Sciences au Sud (Le journal de l'IRD - 62 - novembre/décembre 2011) :

Tous pour un, un pour tous !

Les agriculteurs de l'Altiplano bolivien et ceux de la zone subsahélienne en Afrique ont un défi commun : développer des stratégies de protection intégrée des cultures dans des conditions environnementales extrêmes. Des outils transposables entre ces régions du monde peuvent être envisagés.

« *En ce début de XXIe siècle, la sécurité alimentaire de millions de familles des pays du Sud fait face à de nouveaux défis* », constate Olivier Dangles, écologue en poste à Quito, Équateur. Parmi eux, appliquer une protection intégrée des cultures, à savoir des pratiques culturales non nuisibles à la santé et à l'écosystème permettant de lutter efficacement contre les insectes ravageurs. Dans ce domaine, des agriculteurs de régions pourtant très éloignées peuvent rencontrer des problématiques identiques. L'atelier international sur la lutte contre les ravageurs dans les pays du Sud[1] organisé à Quito, en novembre, a ainsi révélé des défis communs à l'Altiplano bolivien et à la zone subsahélienne. Ces régions sont soumises à des conditions extrêmes – sécheresse, pauvreté des sols, forte saisonnalité – induisant de faibles rendements. « *Dans ce contexte qui laisse très peu de marge aux agriculteurs, la protection intégrée des cultures, pourtant essentielle, apparaît comme un luxe* », observe Olivier Dangles. Et si les défis sont identiques, les moyens dont disposent les pays pour les surmonter ne le sont pas.

« *La protection intégrée des cultures demande une approche multidisciplinaire qui prend en compte l'environnement et l'homme. Mais nous manquons d'outils de modélisation permettant de comprendre la dynamique des ravageurs, notamment* », déplore Malick Niango Ba, entomologiste burkinabé présent à Quito.

Identifier des outils transposables d'une région à l'autre est donc nécessaire. Lors de l'atelier, l'IRD et ses partenaires, porteurs du projet Innomip[2] pour le nord des Andes, ont présenté une base de données en ligne des différents projets régionaux et un modèle couplant dynamiques des agriculteurs et des ravageurs (voir encadré). « *Ce modèle pourrait fonctionner pour d'autres régions, à condition de l'adapter à la réalité sociale du pays qui influe sur les stratégies de lutte contre les ravageurs* », souligne Olivier Dangles. Sur l'Altiplano par exemple, le récent boum de la quinoa a entraîné une expansion des cultures et une migration des populations vers les villes. Alors que l'agriculture subsahélienne reste plus traditionnelle, tournée vers l'auto-consommation.

À l'issue de cet atelier, qui a réuni 20 experts de pays et organisations divers, les bases de la réflexion sont jetées. Afin de l'enrichir, une enquête en ligne a été lancée auprès d'acteurs internationaux de la protection intégrée des cultures. La publication des résultats est prévue pour le printemps 2012.

1. Organisé par l'IRD et l'Université pontificale catholique d'Équateur et soutenu par la Fondation McKnight et la Coopération régionale pour les pays andins.

2. Approches innovantes pour la protection intégrée des cultures dans les Andes, au Pérou, en Bolivie et Équateur : www.innomip.ird.fr

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Protection des cultures et diffusion de l'information

Pour faire face à un ravageur des cultures, il ne suffit pas toujours d'avoir la solution, encore faut-il que cette solution soit adoptée et diffusée au sein d'une communauté d'agriculteurs. Ainsi, le succès d'un programme de lutte dépendra-t-il de l'efficacité avec laquelle l'information se transmet d'un agriculteur informé à un autre. Pour évaluer les conséquences de la diffusion d'une information sur les niveaux de population d'un ravageur des cultures, François Rebaudo et Olivier Dangles ont développé un modèle informatique couplant un système biologique (ravageur des cultures) et un système social (diffusion de l'information entre agriculteurs) dans les Andes équatoriennes[1]. Grace à des données écologiques de terrain et des enquêtes auprès des agriculteurs, les chercheurs ont pu mettre en évidence l'intérêt, pour une communauté d'agriculteurs, de coopérer dans la lutte contre le ravageur via la diffusion de l'information liée à son contrôle. Ces travaux soulignent la pertinence d'une approche socio-écologique afin de prédire au mieux le succès des programmes de lutte contre les ravageurs des cultures, et de manière plus large, de tout programme ayant à trait à la diffusion d'innovations au sein d'une communauté d'usagers.

1. *Plos Computational Biology*, 2011.

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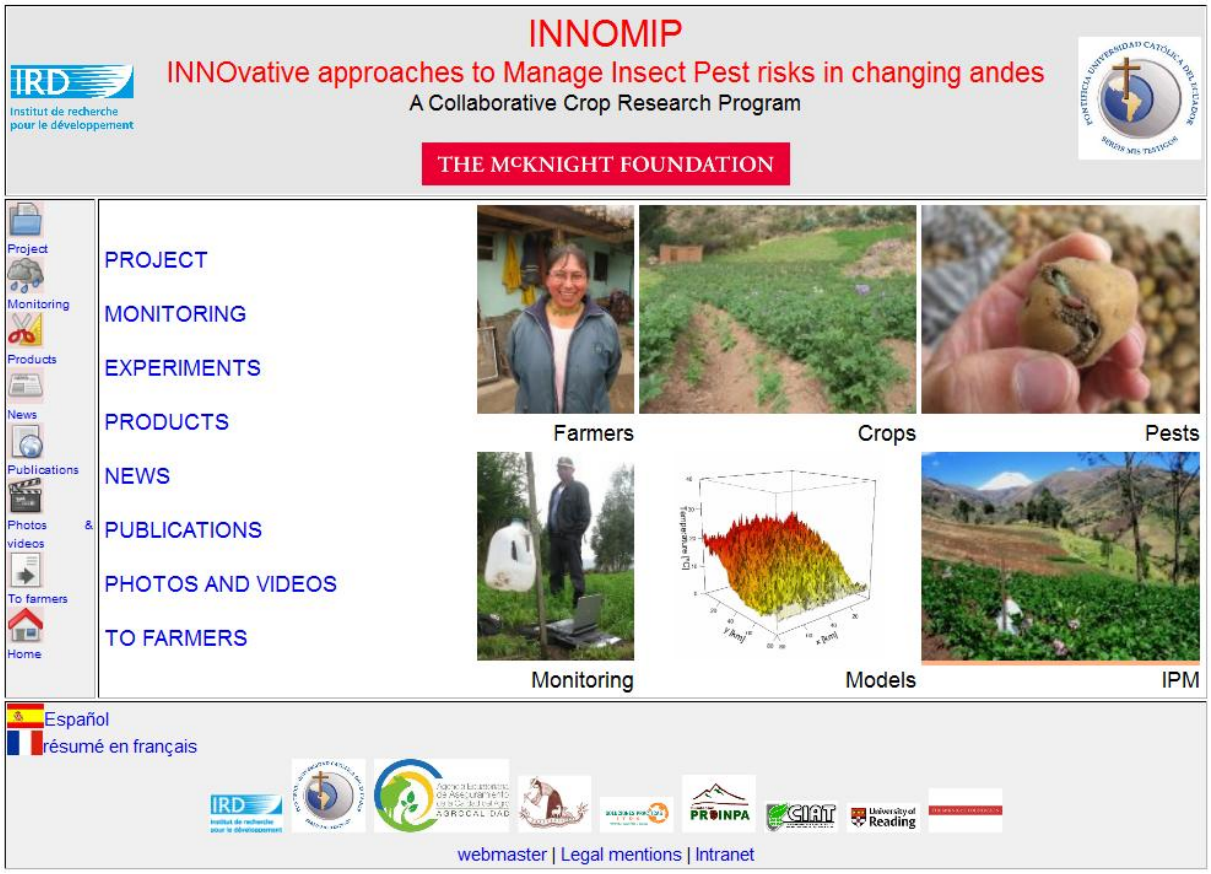
7. Autres productions

7.1. Conception et développment du site Internet http://www.innomip.ird.fr



7.2. Brochures de vulgatisation scientifique

[2] Carpio P, Crespo-Perex V, Herrera M, Barragan A, **Rebaudo F**, Dangles O (2011) Innovaciones para el manejo integrado de plagas en los Andes. PUCE-IRD-Fundacion McKnight, Quito. *http://www.ecuador.ird.fr/content/download/31517/243274/version/3/file/FOLLETO+POLILLAS+PAPA+6+JUL%282%29.pdf*

[1] Carpio P, Herrera M, **Rebaudo F**, Crespo-Perex V, Dangles O (2011) Maneje la polilla de la papa. PUCE-IRD, 12 p.