



Analysis

Towards the integration of spread and economic impacts of biological invasions in a landscape of learning and imitating agents

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ABSTRACT

We develop an agent-based model integrated with a spatial stochastic simulation harmful non-indigenous species (NIS) spread model in which farmers have learning and imitation capabilities. The model is applied to the western corn rootworm (WCR) invasion in the UK. The invasion is never eradicated due to the high dispersal capacity of WCR, particularly under climate change conditions. The lowest expected welfare losses arise with a *laissez faire* policy against the invasion. The effectiveness of NIS control programmes that require participation by land managers is shown to depend greatly on their learning and imitation dynamics. Control programmes might fail completely if there is global knowledge of the burdens of compliance – e.g. through the media – and the land managers can foresee the future consequences of new actions. This is due to coordinated noncompliance occurring across the landscape. If the agents need to experience compliance to learn its consequences or communicate only locally, potential noncompliant behaviour spreads more slowly than the invasion front and trails behind it. In conclusion, negative opinions of land managers over NIS control programmes and their media coverage can strongly undermine programmes. Identification and management of these factors may increase the odds of success of the programmes.

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1. Introduction

International trade and travel generates wealth but is also one of the main factors leading to the introduction of harmful non-indigenous species (NIS) beyond their natural range (Dehnen-Schmutz et al., 2007; Waage et al., 2008). NIS cause considerable ecological and economic impacts that are in many cases correlated (Vilà et al., 2010). For instance, the total costs due to non-indigenous species in the United States (US) have been estimated to be at least \$137 billion per year (Pimentel et al., 2000).

Biological invasions are complex dynamic and spatial processes where ecological and economic factors intertwine at the landscape scale. The development of bioeconomic models that combine invasion ecology with economic analysis tools are of great help both to the control of NIS in general and pests in particular. For instance pest risk analysis, adopted through international standards endorsed by the World Trade Organisation as the rationale under which national agencies may restrict international trade for plant health reasons, requires the estimation of economic costs derived from spread

(FAO, 2004) and must be justified by appropriate risk assessment (MacLeod et al., 2010). One of the most challenging tasks when modelling NIS spread to facilitate policy analysis is to estimate dynamically and spatially the economic impacts derived from the invasion (Baker et al., 2005). Traditional economic modelling approaches for agricultural policy analysis do not facilitate integration with spatially explicit spread models of NIS. The main obstacles are that economic and ecological models present different spatial and dynamic scales (Janssen et al., 2006) and agricultural economics models do not explicitly capture the spatial interactions between individual farmers (Berger, 2001; Nolan et al., 2009), which are especially relevant in the case of NIS spread modelling (Epanchin-Niell et al., 2010).

The body of literature regarding the bioeconomic modelling of NIS spread has increased recently. Bioeconomic models have been developed to identify the optimal allocation of resources between prevention, detection and control activities (Burnett et al., 2008; Carrasco et al., 2010a; Eiswerth and Johnson, 2002; Horan et al., 2002; Perring, 2005; Polasky, 2010; Rout et al., 2011). Established ecological models like reaction–diffusion, stratified diffusion and predator–prey have been integrated with the economic management of invasive pests and weeds (Barbier, 2001; Cacho et al., 2008; Carrasco et al., 2010c; a review is provided by Epanchin-Niell and Hastings, 2010; Sadler et al., 2011; Sharov and Liebhold, 1998) and the analytical spatial

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study of NIS spread and control has been recently approached using metapopulation models (Albers et al., 2010; Sanchirico et al., 2010).

A more accurate estimation of the economic impacts due to the spread of NIS and animal diseases, at the cost of not employing spatially explicit spread models, is attained by bioeconomic models that incorporate partial equilibrium market models of the affected commodity (Cook, 2008; Heikkila and Peltola, 2004; Paarlberg et al., 2003); the export markets (Acquaye et al., 2005; Cook and Fraser, 2008); and that study the flow-on effects of the invasion to the rest of the economy using general equilibrium models (Wittwer et al., 2005). These models present an aggregated and compact nature and maximise a common sector welfare function, making it difficult to integrate them with spatial ecological processes.

The integration of NIS spatial spread models with welfare analysis would allow, in addition, for the consideration of poorly understood spatial interactions between the biological invasion and decisions by land managers. How would the learning and imitation processes among land managers regarding compliance affect the effectiveness of the quarantine campaign? Is behaviour more influential when triggered by the media (e.g. newspapers, television or internet) than when triggered by communication with nearby neighbours? Related to this, NIS quarantine programmes have been described as weakest-link public goods (Perrings et al., 2002); i.e. the control of the NIS depends on the least effective provider, however, this characteristic has neither been tested for the case of spread control programmes using spatially explicit models nor when the land managers can interact.

Flexible modelling approaches that can incorporate the heterogeneity and interactions among land managers and can be integrated with realistic spatially explicit spread models are spatial stochastic simulation and agent-based models (Nolan et al., 2009). Spatial stochastic simulation has been employed to combine NIS spread and economic impacts, for example to study the impacts of NIS in the mountain fynbos ecosystems in South Africa (Higgins et al., 1997); the estimation of the economic impacts of potato brown rot in the potato industry in the Netherlands (Breukers et al., 2008); the efficient allocation of surveillance resources (Cacho and Hester, 2011; Cacho et al., 2010; Stanaway et al., 2010); and the estimation of the impacts of *Sirex noctilio* Fabricius on pine timber supply in eastern Canada (Yemshanov et al., 2008).

Agent-based models (ABM), on the other hand, are computer systems composed of autonomous entities (e.g. representing humans) capable of taking decisions and interacting with the environment and other entities (Bousquet and Le Page, 2004). Originally developed in the field of artificial intelligence, ABMs have been employed for integrating human decisions as components of an ecosystem in several disciplines. Some examples are: CATCHSCAPE to foster discussion between stakeholder in water management conflicts (Becu et al., 2003); PALM that combines farmers decision-making with soil dynamics (Matthews, 2006); GEMACE that assist in the sustainable management of hunting regions (Mathevet et al., 2003); FEARLUS and LUCITA for the modelling of land use dynamics (Gotts et al., 2003; Jepsen et al., 2006); and the use of mathematical programming models combined with agent-based models to study the adoption of agricultural innovations (Schreinemachers et al., 2010). Despite of their potential for the economic modelling of NIS, ABMs have rarely been combined with models of NIS spread and management (Rebaudo et al., 2011). Related to this, the study of the spread of NIS in landscapes of interacting agents is a very new area of research on the economics of NIS management that presents very high potential to derive new insights for NIS control (e.g. Epanchin-Niell et al., 2010; Grimsrud et al., 2008).

Here we develop an ABM coupled to spatial stochastic simulation to link spatially and temporally NIS spread with economic impacts. The farmer agents learning capabilities are modelled with an experience collection (melioration)–imitation algorithm (Brenner et al.,

2006). The model is applied to the case of western corn rootworm (WCR) in the UK. We deal with the specific question: what are the most cost-effective levels of control and detection to be applied against WCR in the UK? Can farmers' imitation and learning processes affect the dynamics of the invasion and under which circumstances?

2. Case Study: Invasion by Western Corn Rootworm in Europe

The WCR, *Diabrotica virgifera* ssp. *virgifera* LeConte (Coleoptera: Chrysomelidae) is an important pest of maize in the USA that is now posing a threat to maize production in Europe. WCR is a univoltine insect that overwinters in the egg stage. WCR larvae attack the roots of maize leading to a decrease of nutrient intake, reduced growth of the plant and a higher risk of lodging (Gavloski et al., 1992). Successful development depends mostly on sufficient maize plants being available within the range of larval movement; hence crop rotation has traditionally been utilised as an effective control measure.

The first introduction of WCR in Europe occurred near Belgrade (Serbia) between 1979 and 1984 (Szalai et al., 2011). WCR rapidly spread throughout central and south-Eastern Europe at rates of up to 60–80 km per year. Since 1998 a number of geographically distant outbreaks have been detected in various countries, including Italy, France, Switzerland, Belgium, the United Kingdom and The Netherlands.

The European Commission (EC) has implemented eradication and surveillance measures aimed at preventing the spread of WCR in Europe (Anonymous, 2003). Emergency measures to prevent the spread of WCR include European Union (EU) Member States conducting official surveys with pheromone traps to detect the presence of WCR in their territories in areas where maize is grown (Anonymous, 2003). Then, when the presence of WCR is newly detected in a field, management measures are applied within radial zones – *buffer zones* – around each infested field (Eyre et al., 2007). They include rotation of maize within demarcated buffer zones in order to reduce the availability of susceptible hosts for WCR larvae and adults. In this study, buffer zones refer to the EC recommended 1 km radius “focus zones” where maize rotation is implemented for two years out of three and insecticide treatment is applied (Anonymous, 2003).

The adoption of the rotation practises suggested by the EC in the UK poses considerable private costs to a large proportion of farmers (MacLeod et al., 2005). The majority of maize grown in the UK is destined for cattle forage, serving as an input to milk and beef production (91%, Table S1 in the Electronic Supplementary material (ESM), with most of the remaining area being game cover maize). Hence, private costs are incurred by farmers having to temporarily adopt alternatives to maize production to restrict the food source for WCR; e.g. buying in maize, using alternative fodders and food supplements, or renting land elsewhere to grow maize. Only a certain proportion of the farmers growing continuous maize present constraints to rotation (Table S1). The constraints are due to the lack of available alternative land or expertise to grow maize, thus leading to the use of alternative crops and increase of production costs (ADAS, 2004).

3. Methods

3.1. General Conceptual Framework

The spread of biological invasions is the result of spatial interactions between the NIS, abiotic (e.g. climate) and biotic environment (e.g. predators) and connectivity of the landscape (e.g. habitat fragmentation, human transport networks) (Fig. 1). Spread results from a combination of population dynamics at habitat patch level and the dispersal mechanisms utilised by the NIS. Considering a NIS impacting a marketable commodity (e.g. agricultural or silvicultural crops); costs are firstly generated at an industry level if its presence leads to the loss of export markets and at field level if its abundance impacts a marketable host or a native harvestable species. At field

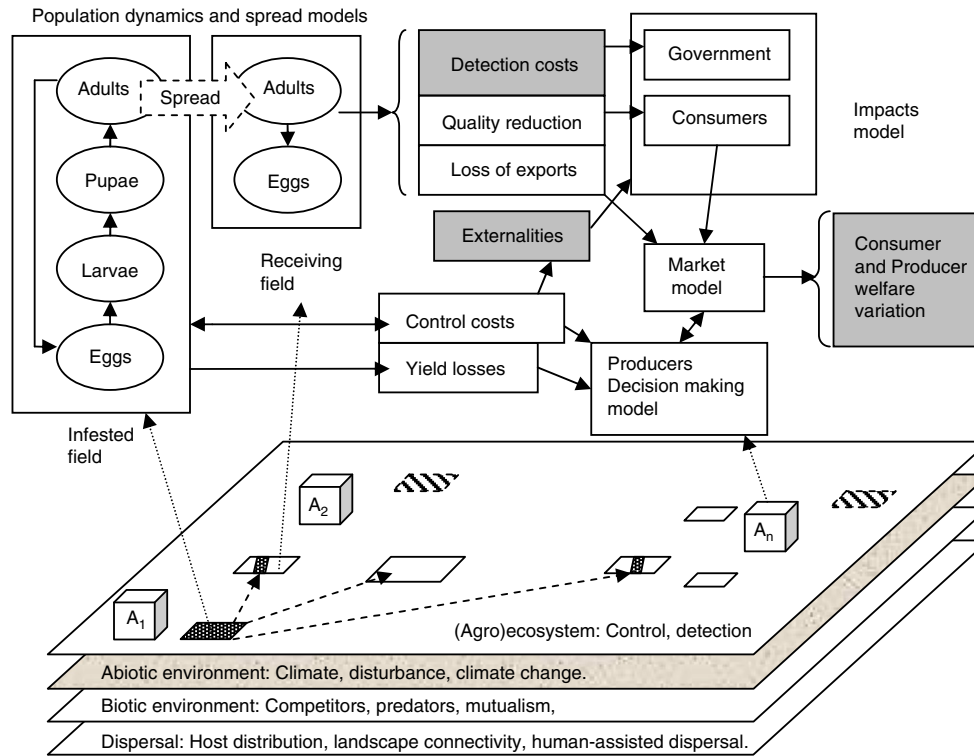


Fig. 1. Conceptual modelling framework representing the components of the models and their context: biological invasions by an insect NIS affecting a host with a market value and spreading in a landscape of interacting land managers. $A_1 \dots A_n$ are land managers of a set of habitat patches.

level, the land manager has the option of controlling the NIS, incurring management costs, or to take no management action and bear the total production losses. The government itself can command the land managers to adopt quarantine measures (that might impose further costs on the producers) or to carry out detection campaigns and statutory control measures which lead to costs borne by society. The spatial aggregation of these costs can be used for further analysis of the dynamic impacts of the NIS using partial equilibrium market models (Fig. S1 in the ESM); and if the shocks of the supply curve can affect other markets, the knock-on effects to the rest of the economy can be estimated using input–output tables.

3.2. Integration of Spatial Spread with Producers' Dynamic Welfare Analysis

An ideal integration of welfare analysis and NIS spread models would demand detailed knowledge of the marginal and average cost functions of the producers across the landscape. This is rarely available due to the sensitive nature of the data. An alternative is to characterise a number of farm types according to short-run (i.e. holding capital inputs constant) average (variable) costs. The approximate individual surpluses of farmers (PW) categorised under these farm types can be calculated as:

$$PW_{it} = Q_{it}(p_t - ATC_{it}(Q_{it})),$$

where Q_{it} is the quantity supplied by farmer i at time t , p_t is the market price and ATC_{it} is the average cost at that level of output (Cook and Fraser, 2002). This way, using the more common spatially disaggregated information on the effect of the NIS on the average total costs of the producers, we can approximate the overall welfare losses of producers and link them to NIS spatial spread models.

3.3. Welfare Variation Due to a WCR Invasion in the UK

The invasion by WCR in the UK corresponds to case of a net importer of the affected host (see ESM section S1 and Fig. S1(b) for a more

detailed description of the general cases). Assuming that the world price will not change, the net present value (NPV) of the variation of producer welfare (ΔPW , FLJ in Fig. S1(a)) can be calculated as:

$$\Delta PW = \int_0^T e^{-rt} \left(\sum_{i=1}^N \Delta PC_i \right) dt \tag{1}$$

where T is the time horizon considered, r is the discount rate, ΔPC_i is the variation of the average private costs of production of farmer i and N is the total number of farmers affected by WCR and the quarantine measures. The overall private costs to farmer i (PC_{ti}) due to WCR are:

$$PC_{ti} = C_{zti} + X_{ti} \tag{2}$$

where X_{ti} are the financial impacts due to compliance with quarantine measures (impacts due to forced rotation) and C_{zti} are the overall control costs at time t , taking into account impacts due to yield losses (YL) for each farmer i :

$$C_{zti} = YL_{ti}(N_{ti}(z)) \cdot p_t + p_z \cdot n_z \cdot A_{ti} \tag{3}$$

where YL are the yield losses that depend on the density of WCR in the field (N) which itself depends on the level of control applied (z , see ESM); p is the price of maize; p_z is the unit cost of control (pesticide, application costs and inspection the previous year per ha); n_z is the number of applications; and A_t is the area where control is applied at time t .

The NPV of the loss of welfare to society (ΔSW) is calculated as:

$$\Delta SW = \int_0^T e^{-rt} C_{St} dt \tag{4}$$

where C_{St} is the detection cost (given a level of surveillance S , see ESM) in the time period t .

4. Farmer Agent Decision-Making

The set of decisions that are available for a farmer are influenced by behavioural constraints that reflect personal experience and observations of neighbours' experiences (Berger, 2001; Nolan et al., 2009). Based on experimental psychology, the farmer agents in the model were endowed with the capacity to learn from past experiences (melioration, Herrnstein and Prelec, 1991) and imitate successful strategies in their neighbours (Rumiati and Bekkering, 2003).

We employed a melioration-imitation model (Brenner et al., 2006). Eq. (5) represents the dynamics of melioration learning that is used here to represent routine-based learning of experience collection:

$$\frac{dp(\omega, t)}{dt} = p(\omega, t) \left(\bar{u}(\omega, t) - \sum_{\tilde{\omega} \in \Omega} p(\tilde{\omega}, t) \bar{u}(\tilde{\omega}, t) \right) \quad (5)$$

where $p(\omega, t)$ is the probability of adopting strategy ω at the time t and it is endogenously calculated through comparison with the neighbours' strategies and their payoffs; $\nu(\cdot)$ is a monotonously increasing utility function where $\nu(0) = 0$ (for simplicity we assume ν to be a linear function); $\tilde{\omega}$ are the rest of alternative strategies and are represented by the set Ω ; and $\bar{u}(\omega, t)$ is the average payoff of strategy ω .

We assume that the agents take into account their own past payoffs when adopting strategy ω and also have the capacity to communicate with their neighbours within a distance D to ask them about their payoffs when they are also adopting strategy ω (e.g. Eshel et al., 1998). We model the average payoff as (Brenner et al., 2006):

$$\bar{u}_i(\omega, t) = \frac{1-\beta}{1-\beta^{(t-1)}} \sum_{\tau=0}^{t-1} \left[\beta^{(t-1-\tau)} (1-\sigma) \cdot u_i(\tau, \omega) \cdot \sigma \cdot \sum_{j=1}^{N/d_j \leq D} u_j(\tau, \omega) \cdot N^{-1} \right] \quad (6)$$

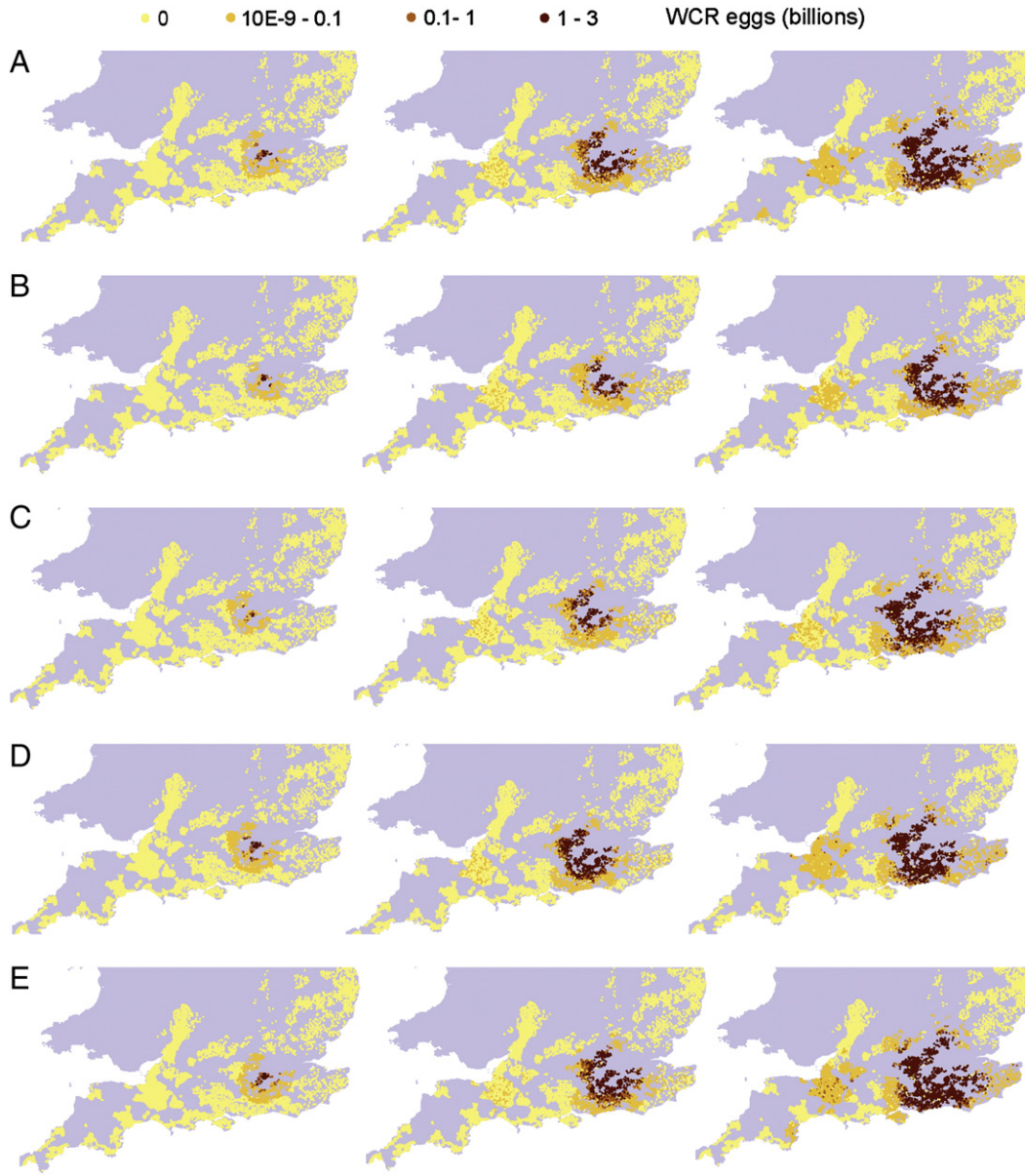


Fig. 2. Maps of the spread of WCR in the UK under 2030 projected temperature conditions and human-assisted long-distance dispersal events. The colours represent the number of WCR eggs in the field in winter (billions). A: no control; B: neither imitation nor learning and control policy using buffer zones of 15 km radius; C: control policy under a "local communication" scenario and naïve farmers; D: control policy under a "local communication" scenario and interpreter farmers; and E: control policy under a "media communication" scenario and interpreter farmers. From left to right the maps correspond to the 10th, 15th and 20th year of the invasion respectively.

Eq. (6) is an exponentially weighted average of the own past experience of the agent i and the experience of all the neighbours j within a distance of agent i ($d_{ij} < D$) that adopted strategy ω when $t = \tau$; $u_i(\tau)$ and $u_j(\tau)$ are the average payoffs obtained by the agent i and the neighbour j respectively; σ is the weight with which agent i incorporates the experience of agents j in the formation of expectations about the future payoff; β is a parameter reflecting the time horizon of memory.

In our application to WCR invasion in the UK, the agents can decide upon two main actions: compliance or non-compliance with quarantine regulations and application of insecticide control against the NIS or not (see the ESM for a detailed description of the modelling of farmers' decision-making).

4.1. Model Structure and Software

The model was programmed using the object oriented programming paradigm in the Java language (<http://java.sun.com>). Fig. S2 in the electronic Supplementary material (ESM) demonstrates the structure of the model using a Unified Modelling Language class diagram. The model is composed of the classes: *World*, *Government*, *Field* and *Farmer*. The class *World* extends the interface *SimModel* from the Repast agent-based modelling toolkit (North et al., 2006) and the class *Farmer* extends the interface *GisAgent* from the SLUDGE model (Parker and Meretsky, 2004). Both *Farmer* and *Government* classes are connected to each other and to the *Field* class (Fig. S2 in ESM).

A nested loop is used to structure the model (Fig. S4). At the beginning of the annual loop the inspected fields (where the pheromone traps are located) are endogenously determined together with the buffer zones by the government agent. On further nested loops the population dynamics of the colonies of each field are determined according to temperature. Natural and human-assisted dispersal are simulated in a daily and seasonal loop respectively.

A description of the components of the model using the Overview, Design concepts, and Details protocol (Grimm et al., 2010) for its reproducibility can be found in the ESM: spatial and human-assisted long-distance dispersal events (LDDE); spatial detection and control measures by the governments; private control strategies and associated costs; compliance of the farmer and associated costs; and the phenology sub-models for the host and the NIS in each field. Further details describing the dispersal and phenology models, their parameterization and validation can be found in Carrasco et al. (2010b).

5. Simulation Experiments

The model was initialized infesting fields in the vicinity of Heathrow airport (London) (Eyre et al., 2007) (see ESM for a description of the input data) and run under climate change projections corresponding to 2030 (Hulme et al., 2002). The model was run under two main hypothetical scenarios (Table 1 describes the specific simulation experiments undertaken): (1) the farmer agents are passive and do not present learning and imitation capabilities and (2) the farmer agents

have learning and imitation capabilities (Table 1, “learning-imitation” no and yes respectively). The model was simulated to explore:

- (i) the effect of varying buffer zone radius, detection budgets and the dispersal capability of WCR on the net discounted producers' welfare losses and cumulative area invaded;
- (ii) the effect of farmers being able to foresee the economic burden that compliance will have on them (“interpreters”) before complying versus farmers that only realise the burden once they comply with the quarantine programme (“naïve”)
- (iii) the effect of farmers having instantaneous general knowledge about the situation of all the farmers (“media scenario”) versus farmers only learning about the compliance burden from neighbours (“local communication scenario”).

6. Results

6.1. Simulation Experiment 1: Optimal Management of WCR in the UK

Eradication of the main invasion was not achieved in any of the scenarios examined due to the high mobility of WCR and the favourable climatic conditions in the simulations.

In the case of passive farmers without learning and imitation capabilities, the lowest producer welfare losses corresponded to a *laissez faire* policy. For a control policy, on the other hand, the total costs increased for stricter control measures (Fig. 3(A) to (C)), even though stricter control measures led to a smaller area invaded (Fig. 3(D) to (F)). A trade-off between costs due to compliance and yield losses was observed: the stricter the control policy the lower the yield losses but the higher the compliance costs (Fig. 3(B) and (C)). The management of NIS invasions might present several economic local optima: eradication, slowdown and “do nothing” (Sharov and Liebhold, 1998). If an interior solution existed, the optimal policy that would minimise the expected welfare losses would be one in which the marginal costs of control and marginal avoided costs due to yield losses and private control (marginal benefits of control) were equal. However, the marginal costs of control are greater than the marginal benefits of control even for very small buffer zones (Fig. 3(A)). The model presents a corner solution at zero width buffer zones (*laissez faire* or “do nothing” scenario). A second interior solution corresponding to slowdown or eradication could be expected if, for very large buffer zone widths, total costs decreased. However, for the wide range of buffer widths considered – up to 15 times greater than the 1 km “focus zone” radius recommended by the EC (Anonymous, 2003) – total costs did not decrease (Fig. 3(A)), and slowdown or eradication could not be identified as optimal.

The attractiveness of the *laissez faire* strategy was due to the lower revenue loss due to rotation measures. A strict policy, however, produces beneficial outcomes by slowing down the invasion and keeping population density low, thus avoiding yield losses and associated management costs. Because the extent of the invasion remains smaller through time (Fig. 2 comparing scenarios A and B), fewer farmers

Table 1

Simulation experiments, effects studied and main results. *Interpreter farmers*: farmers are able to foresee the economic burden that compliance will have on them. *Naïve farmers*: farmers that only realise the burden once they comply with the quarantine programme. *Media communication*: farmers have instantaneous general knowledge about the situation of all the farmers. *Local communication*: farmers only learn about the compliance burden from neighbours.

Simulation experiment	Learning-imitation	Effects studied	Results
1 (Fig. 3A, D)	No	Baseline parameter values	Lowest welfare losses for no control. Decreasing cumulative area invaded with stricter control.
2 (Fig. 3B, E)	No	Dispersal capacity	Welfare losses and area invaded increase for higher dispersal capacity.
3 (Fig. 3C, F)	No	Detection budget	Welfare losses increase for higher detection budget. Cumulative area invaded increases for lower detection budget.
4 (Fig. 4A, C)	Yes	Local and media communication with naïve farmers	Undetermined effect of local and media communication. Welfare losses relatively similar to experiment 1: similar effectiveness of control programme under naïve farmers.
5 (Fig. 4B, D)	Yes	Local and media communication with interpreter farmers	Interpreter farmers–media communication leads to very high ineffectiveness of the control programme. Interpreter farmer–local communication is economically inefficient and leads to very high welfare losses.

are forced into costly rotation while yield losses to the remaining farms are avoided. Given that a *laissez faire* policy has a lower level of producer welfare losses than strict measures it is the preferred option. The performance of a *laissez faire* strategy is not affected by potential noncompliance. On the other hand, strict control measures have a risk of failure associated with noncompliance, and even if total compliance occurred – which would make the policy independent of learning and imitation dynamics – control measures would not outperform a *laissez faire* scenario (Fig. 3(A) to (C)).

6.2. Simulation Experiment 2: Effects of Dispersal Capacity of WCR

Higher dispersal capacity of WCR led to a higher NPV of producer welfare losses (Fig. 3(B)), an increase in the maximum from £5.5 to £8 million in the case of a median scale of the dispersal kernel increasing from 100 m to 2000 m and higher cumulative area invaded (Fig. 3(E)).

6.3. Simulation Experiment 3: Effects of Detection Budget

For greater detection budgets, the NPV of welfare loss increased and the cumulative area invaded decreased (Fig. 3(C) and (F)). The increase in welfare loss is due to greater detection and thus enforcement, leading to higher compliance costs (Fig. 3(C)). Low detection budgets led to a higher area invaded (Fig. 3(F)) because a larger proportion of infested fields were neither detected nor controlled.

7. Effects of Imitation and Learning

7.1. Simulation Experiment 4: Naïve Farmers Under Local and Media Communication

When the farmers are “naïve” – needed to experience the burden of compliance to form an opinion about it – the control programme was effective (Fig. 2 where A and C are very similar). There was no clear effect of the type of communication: local contact or global media (Fig. 4(C)). The reason was that farmers needed time to build up an opinion against compliance and this would not allow noncompliance spreading as fast as the invasion front.

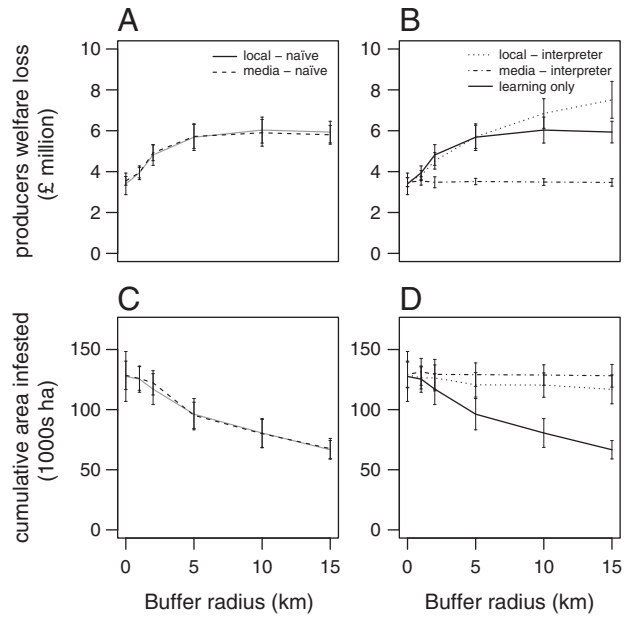


Fig. 4. Net present value of producers' welfare losses and cumulative area invaded due to WCR invasion under different buffer zone radius lengths when: (i) the farmers can or cannot predict the economic implications of compliance (“interpreter” and “naïve” respectively); (ii) communication between farmers occurs at a local level or information is shared globally by the media (“local” and “media” respectively); and (iii) the farmers can only learn from their own experience but cannot imitate other farmers (learning only). The error bars represent one standard deviation.

When the farmers are “naïve”, most of the farmers at the invasion front comply with controls, leading to lower welfare losses (Fig. 4(A)). This situation leads to results similar to the baseline passive farmers scenario (Figs. 4(A) and 3(A)).

7.2. Simulation Experiment 5: Interpreter Farmers Under Local and Media Communication

We found that control measures were very ineffective in terms of containing the invasion under the “media”-“interpreter” farmer

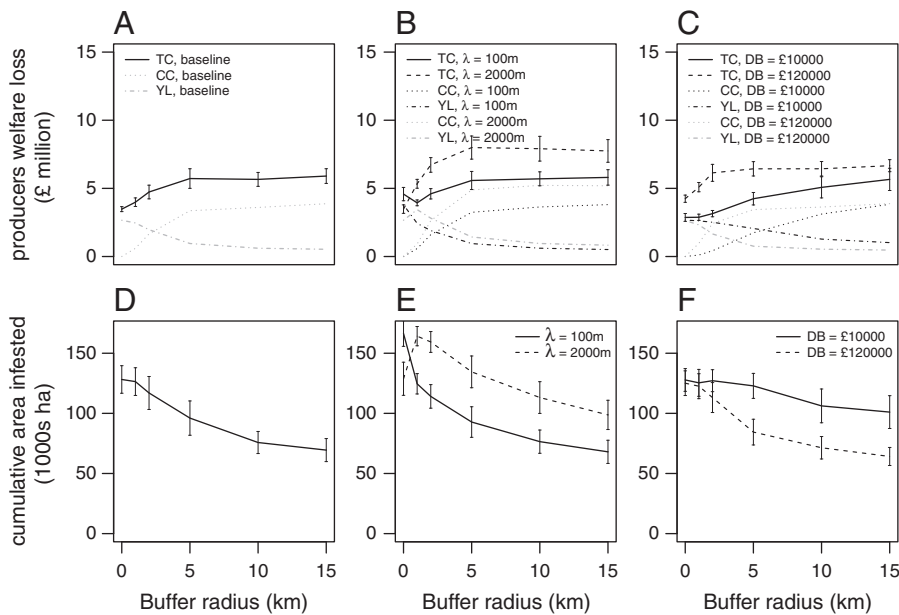


Fig. 3. Baseline parameters scenario (baseline) and effect of the budget of detection (BD) and natural dispersal kernel scale (λ) on the net present value (NPV) of producers' welfare losses and cumulative area invaded due to WCR under different buffer zone radius lengths. Otherwise stated, the baseline parameters are: λ = 300 m; BD = £ 60,000; TC: NPV of total welfare losses; YL: NPV of costs due to yield losses; CC: NPV of compliance costs. The error bars represent one standard deviation.

scenario (Fig. 4(D) compared to (C)) because in this scenario sudden landscapes of noncomplying farmers occurred. This led to a situation similar to a *laissez faire* scenario (Fig. 2A compared to E). Farmers could foresee that compliance was burdensome to them and spread the opinion among their neighbours even before the invasion reached them. The effectiveness of the control was higher – but still very low – when the farmers were “interpreters” but only local communication occurred (Figs. 4(D) and 2D where this scenario is very similar to the *laissez faire* scenario in A). In this situation the farmers could rapidly turn to noncompliance once triggered by neighbours recognising the burdens of compliance. This situation was very inefficient in terms of welfare losses (Fig. 4(B) with a maximum of £7.5 million compared to the same scenario with passive agents leading to only £5.9 million). The WCR populations increase due to noncomplying farmers behind the invasion front and are more likely to successfully invade new fields and leading to more farmers having to comply.

7.3. Compensation to Farmers with Constraints to Rotation

A full compensation scheme in which the government would pay back the costs of compliance to farmers with constraints to rotation would cost £3.8 million – assuming no extra administrative costs and no compensation to farmers without rotation constraints. This scheme would avoid the spread of noncompliance behaviour (Fig. 4) and would in effect lead to the equivalent baseline passive farmers scenario (Fig. 3A). A compensation scheme would be attractive in improving the outcome in the case of local communication and farmers anticipating effects (Fig. 4(B) “local–interpreter” scenario) because it could reduce producer welfare losses substantially.

8. Discussion

The simulation experiments generated new unexpected NIS management insights when considering the behaviours of the farmers through the landscape. The control of a spreading WCR invasion with burdensome spatial quarantine measures could be ineffective when the farmers could foresee the implications of compliance and obtain information from the media. Conversely without a capacity to foresee the consequences of their actions and under only local communication the programme was still effective.

The fact that the effectiveness of control programmes might depend, in a complex manner, on the behavioural and spatial dynamics of the farmers appears to contradict that invasive species control is a weakest-link public good (Perrings et al., 2002) in the case of spread control. In light of the results, we would contend biosecurity can only be considered as such in instances where a NIS is spreading extremely rapidly (almost instantaneously, in fact) and where a loss of area-freedom from a NIS causes export market restrictions. In our case study, we show that, even in the case of a formidable disperser such as WCR (Coats et al., 1986), biosecurity programmes focusing on slowing down an invasion are not necessarily undermined by the decisions of one farmer but vary depending on the responses and behaviour of the population in a complex manner.

The policy implication is that plant health agencies might not need to allocate a large share of their resources to the verification and enforcement of individual compliance if a NIS is already spreading but to try to ascertain the general opinions and behavioural dynamics of the farmers' population. Indicators that a quarantine programme will not be undermined by noncompliance might be absence of negative opinions (or even absence of opinion) among land managers and the media. This approach would be very much along the lines of current research funding efforts from the US national security agencies for the prediction of social instability (e.g. riots, political turmoil and the outbreak of wars) using social networks like “Twitter” (Weinberger, 2011a,b).

Regarding the specific case of WCR in the UK, a trade-off between compliance costs and yield losses was observed, although a *laissez faire* policy presented the lowest welfare losses and was preferred. Strict measures might be controversial for the farmers, but would lead to substantial avoidance of yield losses. These results illustrate how our modelling approach is especially suitable to foster discussion between policy makers and stakeholders. Farmers in the UK might prefer no institutional measures to be implemented due to their associated economic burdens, but at the same time policy makers might advocate for an attempted eradication policy. The surprising answer is that due to such trade-offs between compliance costs and yield losses both groups could be, to a certain extent, right. In the same way that “too many cooks spoil the broth” a compromise between the two solutions could be worse if a situation where a partial building up of noncompliance arises (e.g. as observed in the local communication–interpreter farmer scenario).

In general, further welfare variations can occur due to shifts in the demand curve. For instance, consumers might react adversely to the purchase of the host commodity when the infestation is taking place (e.g. in the case of animal diseases, Paarlberg et al., 2003) or the NIS might reduce the quality of the commodity, e.g. citrus canker in oranges (Acquaye et al., 2005). In the case of agricultural products, the spatial location of the consumers is not as relevant as the producers since they do not directly interact with NIS spread. The consideration of the spatial distribution of consumers might, conversely, be relevant to estimate the impacts for recreational demand of ecosystem services, e.g. native fishes in lakes that are displaced by other invasive species might affect the demand for angling in those lakes (Sun, 1994) and that in turn might contribute to the long-distance dispersal of the NIS (Bossenbroek et al., 2007).

It is increasingly necessary to reconcile NIS spatial spread models with economic models that reflect the market behaviour of the affected commodity, the mitigating measures of producers (Holmes et al., 2009) and their interactions. Our work represents a step towards this goal although further work in this area of research is needed. A perfect reconciliation would require knowledge of the variation of the production and cost functions of the individual producers across the landscape. This information would allow for the bottom-up construction of the supply curve and the ready simulation of the supply shocks as the invasion progresses spatially. Due to data paucity, our approach approximates producers' welfare losses as variations in their average total costs of production due to the NIS. However, if the data were available, the model would be amenable to incorporate further individual producers' information.

Data paucity is also present in the modelling of the potential behaviours and interactions of farmers during the invasion. We based our model of farmers' behaviour on established experimental psychology theories that have been validated experimentally (Herrnstein and Prelec, 1991; Rumiati and Bekkering, 2003); however, field data collected during the spread of an invasion would be very beneficial to calibrate the model. Our modelling approach for the range of farmer' behaviour – assuming optimization of resulting payoffs – should thus be regarded as a theoretical benchmark against which to compare alternative behavioural forces at play. In reality, behaviours based on sense of responsibility or fear of receiving a penalty for noncompliance – even though this is not part of the EC measures against WCR – might lead to low levels of non-compliance. Future research should focus on the collection of empirical observations of the main behaviours and interactions of the land managers occurring during biological invasions.

9. Conclusions

We developed a model that illustrates how spatial stochastic simulation integrated with agent-based models can be used to estimate the economic impacts of a NIS and the implications of farmer interactions and behaviour. Our results have implications for the

management of NIS invasions that involve participation by land managers: negative opinions of land managers about NIS control programmes and their media coverage might be an important factor in the failure of eradication and control programmes. Checking the opinion of land managers on costs and efficacy before the implementation of eradication campaigns would help to allocate resources to those campaigns that are likely to be well-received, and thus present higher odds of success. In addition, negative publicity from the press towards a campaign can be a predictor of campaign failure, allowing for rapid reallocation of resources to other campaigns.

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Appendix A. Supplementary data

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