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Optimal Control of Spreading Biological Invasions: For How Long Should We Apply the Brake?

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Abstract

Identifying the optimal switching point between different invasive alien species (IAS) management policies is a very complex task and policy makers are in need of modelling tools to assist them. In this paper we develop an optimal control bioeconomic model to estimate the type of optimal policy and switching point of control efforts against a spreading IAS. We apply the models to the case study of Colorado potato beetle in the UK. The results demonstrate that eradication is optimal for small initial sizes of invasion at discovery. High capacity of the agency to reduce spread velocity for several years leads to smaller total overall costs of invasion and makes eradication optimal for larger sizes of initial invasion. In many cases, it is optimal to switch from control to acceptance within the time horizon. The switching point depends on the capacity of the agency, initial size of invasion, spread velocity of the IAS and the ratio of unit cost of damage and removal. We encourage the integration of the dispersal patterns of the invader and the geometry of the invasion in the theoretical development of the economics of IAS invasion management.

Keywords: barrier zone, biosecurity, dynamic optimization, eradication, *Leptinotarsa decemlineata*, pest risk analysis, reaction-diffusion.

JEL codes: Q1; Q28; Q57

Introduction

The introduction of invasive alien species (IAS) is one of the main causes of the loss of global biodiversity. IAS lead to extinction of vulnerable native species through predation, grazing, competition and habitat alteration (Mack *et al.*, 2000). In addition, IAS pose great costs to agricultural production, inflicting an increase in pest management expenditures, yield reduction, losses of consumers and producers welfare and loss of export markets.

The different stages of the IAS invasion are entry, establishment and spread. Depending on which stage the invasion is at, these different management decisions would need to be taken by government agencies in charge of managing IAS invasions: prevention, eradication, containment, slowing down and/or acceptance of the invasion[1]. Identifying the optimal policy and switching point between different management policies is a very complex task and the government agencies are in need of modelling tools to assist them. Bioeconomic modelling of IAS management attempts to facilitate those decisions by estimating the optimal policy combination that minimises the total costs of removal and total costs of damage caused by the invasion for a specific time horizon.

Great insight has been gained on the bioeconomics of IAS management in recent years. Analytical models have been devoted to the optimal allocation of resources for preventative measures (Horan, *et al.*, 2002) or after the IAS has been established in order to determine when eradication is the optimum policy (Eiswerth and Van Kooten, 2002; Olson and Roy, 2002; Odom *et al.*, 2003; Burnett *et al.*, 2007). Other approaches more integrative of the invasion stages have focused on assessing the optimal trade off between exclusion and control efforts (Leung *et al.* 2002; Olson and Roy, 2005; Kim *et al.* 2006; Finnoff *et al.*, 2007).

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[1] We define the following IAS management measures as follows: (i) prevention: aimed at reducing the probability of entry and establishment of an IAS; (ii) eradication: aimed at driving the population of the invader to extinction; (iii) containment: aimed at maintaining the invasion at a constant size; (iv) slowing down: aimed at reducing the spread velocity of the invasion whilst allowing it to expand its range; (v) acceptance: to stop managing the invasion and to allow it spread at its natural spread velocity. In this paper, any management measure applied to the invasion after its establishment will be referred to as a "control measure".

These modelling approaches have largely concentrated on IAS population dynamics instead of using theoretical spread models for IAS (e.g. see spread models by: Fisher, 1937; Skellman, 1951; Andow *et al.*, 1990; Shigesada, 1995). Thus, few bioeconomic analytical models take into account the geometry of the invasion. Instead, demographic models are in some cases employed as substitutes for spread models (e.g. logistic growth model). However, demographic models alone are unlikely to provide accurate predictions of invasion spread rates because, in order to relate population growth to spread velocity, it is necessary to take into account the spatial dispersal patterns of the invader (Higgins and Richardson, 1996). Some notable exceptions of bioeconomic models that consider the dispersal patterns of the invader are those that incorporate the spread predictions of reaction-diffusion (R-D) models (constant asymptotic spread velocity) into the management of invasions using barrier zones (e.g. Sharov and Liebhold, 1998; Sharov, 2004; Cacho *et al.*, 2008)[2].

R-D models (Fisher, 1937, Skellman, 1951) are probably the most widely used IAS spread models and have been applied successfully to predict invasion rates from animal species (Levin, 1992). R-D models are partial differential equations where random diffusion in a homogeneous environment is assumed. The main parameters are ε, the intrinsic rate of population growth and D, the diffusivity of the population. For instance the Skellman model is of the form:

$$\frac{\partial n}{\partial t} = D\left(\frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2}\right) + \varepsilon n, \tag{1}$$

where the left hand side in equation (1) represents the change in population density (n) at time (t) and spatial coordinates (x,y) that is caused by random diffusion (first term of the right hand side) and local population growth (second term of the right hand side). The solution of the R-D model is:

$$c = \sqrt{4\varepsilon D}, \tag{2}$$

by which spread is predicted to follow a continuous expansion at an asymptotically constant radial velocity represented by *c*.

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[2] A barrier zone is defined as the area bordering the expansion front of the invasion where management activities are carried out with the aim of reducing the velocity or even to lead to eradication of the invasion. For example, moving barrier zones were employed for the eradication of the boll weevil (*Anthonomous grandis*) in the United States (Sharov, 2004).

Case study: Risk of Colorado potato beetle invasion in the UK

The Colorado potato beetle (CPB) *Leptinotarsa decemlineata* (Say) (Insecta: Coleoptera: Chrysomelidae) is the most important pest of potato (*Solanum tuberosum*) in most areas of North America. CPB also affects other *Solanum* species widely present in the UK. Adults are capable of flying up to 3km and their dispersal can also be assisted by weather events and commercial traffic (Bartlett, 1980; Waage, *et al.*, 2005). For instance, CPB adults arrived *en masse* from Poland and Germany into southern Sweden (Wiktelius, 1981). CPB was inadvertently introduced in Western Europe apparently during World War I. As a result, CPB is now established in large areas of Europe with the exception of the United Kingdom (UK), Ireland, Sweden, Finland and some Spanish and Portuguese islands (Heikkila and Peltola, 2004). The European and Mediterranean Plant Protection Organisation (EPPO) declares CPB as present in the EPPO region but not widely distributed and recommends it be controlled as a quarantine pest (EPPO, 2009). Thus most of the uninfested regions present protected zones against invasion by CPB.

The UK has adopted a successful policy of prevention and eradication of any breeding colonies of CPB since 1877. Breeding colonies have been eradicated during the years 1901-02, 1933-34, 1946-52 and 1976-77 and non-breeding individuals are intercepted in imported vegetable produce almost every year (Bartlett, 1980). These interceptions reflect the permanent risk that CPB represents to the UK potato industry. This risk is increasing: under climate change projections the potential range for the development of CPB in the UK is estimated to increase by 102% (Baker *et al.*, 1996). Hence an increase in the occurrence of breeding colonies and corresponding eradication campaigns is expected.

Whereas the benefits of living without CPB have been demonstrated in the cases of the UK (Mumford *et al.*, 2000; Waage *et al.*, 2005) and Finland (Heikkila and Peltola, 2004), eradication campaigns are very costly and it is necessary to know how long they are justifiable for.

In this paper, we develop a bioeconomic optimal control model where an already established IAS spreads following R-D and a moving barrier zone is considered for

the management of the invasion. We apply the model to the case study of potential CPB invasion in the UK. We build upon the work of Sharov and Liebhold (1998) using instead an optimal control approach and imposing a constraint on the control measures. We consider four main scenarios: Scenario A (C): introduction at the centre of the susceptible range and spread under current climate conditions (climate change projections); scenario B (D): introduction nearby the coast and spread under current climate conditions (climate change projections). The outcome of the study is a bioeconomic model to identify the optimal type of policy and time at which to stop control efforts against an IAS invasion.

Methodology

Policy problem: when to stop control measures

We consider the optimal control problem: whether to control or accept an already established IAS that is spreading following a R-D model (equation (2)). A homogeneous landscape is assumed. Therefore, the asymptotic radial velocity of spread c is constant in every direction, leading to a circular (or fraction of circle) invasion front that is centred at the initial establishment point. In addition, the total area susceptible to be invaded (susceptible range) is assumed to be well approximated by a circle or fraction of circle. Hence, the circular shape of the invasion front holds for all time t. The control variable of the problem (variable over which the agency has the capacity to influence) is u, aimed reduction of spread velocity. u is the consequence of removal activities by a moving barrier zone. The state variable is x, radius of the area invaded. At the moment of discovery the invasion has a size of $x = x_0$ due to undetected spread. We assume that c is constant for all $x > 0$ and $c = 0$ for $x = 0$ (eradication) and $x = x_{max}$ (total susceptible range is invaded).

The problem for the government agency is to minimise (transformed into a maximisation problem by multiplying the objective function by minus one) the net present value (NPV) of the total overall costs (total costs of removal of the invasion and the total costs of damages caused by the IAS in the remaining area invaded, $L(x,u)$):

Maximise L where $L\left(x,u\right) = \int_0^T -e^{-rt}\left(D\left(x(t)\right) + R\left(x(t),u\right)\right)dt$. (3)

Subject to:

$$\frac{\partial x}{\partial t} = c - u$$ (4)

$$0 \leq u \leq u_{max}$$ (5)

$$0 \leq x \leq x_{max}$$ (6)

$$x\left(0\right) = x_0,$$ (7)

Equation (3) is the objective function where T = time horizon, r = discount rate, $D(x(t))$ = total costs due to damage caused by the IAS and $R(x(t),u)$ = total costs of removal of the IAS; equation (4) is the equation of motion of the size of invasion; equation (5) is the restriction of non-negativity of the control variable and the maximum value that u can take (u_{max}) which represents the agency's maximum spread velocity reduction capability; equation (6) is the requirement of non-negativity of the state variable x and the constraint by which x cannot be bigger than the maximum susceptible area; and equation (7) is the initial boundary condition.

The agency can decide to spend resources at any point in time in order to make: (i) $u > c$: the invasion size will decrease and eventually might be eradicated; (ii) $u < c$: the invasion will be slowed down; (iii) $u = c$: the size of invasion will remain the same and (iv) $u = 0$: the invasion is accepted and spreads at its natural velocity.

We assumed the following empirical forms for D(x) and R(x,u):
Damage function: *D(x)* is assumed to follow a linear relationship with the area invaded. The rationale behind this assumption lies in that the impact of an invasion can be estimated by: $I = R \cdot A \cdot E$ (where I stands for overall impact of the invasion, R is the size of the invasion, A is the average abundance and E is the effect per biomass unit of the invader) (Parker, 1999). In our case:

$$D(x) = \frac{D^* \pi x^2}{k} \tag{8}$$

where D^* is the unit cost of damage caused by the IAS per unit of area invaded at the average population abundance. D^* is assumed to be constant and independent of x. k in (8) and (9) denotes the proportion of the circular invasion front that can spread without physical barriers (e.g. $k = 1$ if the introduction occurs in the middle of the susceptible range and $k = 2$ if it occurs near a straight coast line that leads to a semicircular invasion. See Figure 1 for illustration).

Total costs of removal in the barrier zone: *R(u,x)* is proportional to the length of the invasion front ($2\pi x/k$) times the unit cost of removal of an infested unit of area (p_R, that encompasses the unit cost of detection and control activities performed per unit of area) and the aimed reduction of spread velocity ($C(u)$) (Sharov, 2004). We assume that $C(u) = u$ and that p_R is independent of x and constant:

$$R(u,x) = \frac{2\pi x u p_R}{k}. \tag{9}$$

Optimal control

We employ a current value Hamiltonian using the transformations (Chiang, 1992):

$$\lambda_c = \lambda e^{rt} \tag{10}$$

and

$$H_c = He^{rt}.$$

Taking into account the constraints, the resulting current value Lagrangian-Hamiltonian equation is:

$$H_c = \left[-D(x(t)) - R(x(t),u)\right] + \lambda_c(t)[c-u] - \theta[c-u] - \phi[c-u]. \tag{11}$$

Applying the Pontryagin maximum principle the following set of conditions can be obtained:

$$\underset{u}{Max}\, H_c(x,u,\lambda,\theta) \text{ for all } t \in [0,T] \tag{12}$$

$$\frac{dx}{dt} = \frac{\partial H_c}{\partial \lambda_c} = c - u \tag{13}$$

$$\frac{\partial \lambda_c}{\partial t} = -\frac{\partial H_c}{\partial x} + r\lambda_c \tag{14}$$

$$\lambda_c(T) = 0; \tag{15}$$

$$x(T)\, free.$$

$$\frac{\partial H_c}{\partial \theta} = -(c-u) \geq 0 \tag{16}$$

$$\theta \geq 0 \qquad \theta(u-c) = 0$$

$$x \geq 0 \qquad \theta x = 0$$

$$\theta' \geq 0 \qquad (\theta' = 0 \text{ when constraint not binding})$$

$$\frac{\partial H_c}{\partial \phi} = -(c-u) \geq 0 \tag{17}$$

$$\phi \geq 0 \qquad \phi(u-c) = 0$$

$$x \leq x_{max} \qquad \phi x = 0$$

$$\phi' \geq 0 \qquad (\phi' = 0 \text{ when constraint not binding})$$

Equation (12) indicates that the optimal control $u^*(t)$ must maximise the Lagrangian-Hamiltonian for all t within the time horizon considered; (13) is the equation of motion for x; (14) is the equation of motion of the costate variable λ_c modified for the current value Hamiltonian; (15) are the transversality conditions for a vertical terminal line at $t = T$; equations (16) and (17) are the conditions due to the constrained state variable (equation (6)). The complementary-slackness conditions state that θ and φ, the Lagrangian multipliers, will be zero unless $x = 0$ and $x = x_{max}$ respectively (the state constraints become binding).

We initially assume that constraints (16) and (17) are not binding for all t and solve the problem as an unconstrained problem. Given that H_c is linear in the control variable u, we obtain a bang-bang solution for u (Clark, 1990). $\partial H_c/\partial u$ is called the switching function and is referred to as σ. To maximise H_c, the boundary solution $u^* = 0$ (acceptance of invasion) should be chosen if σ is negative and $u^* = u_{max}$ will be chosen if σ is positive. Only if $\sigma = 0$ for a positive interval of time, the Hamiltonian does not depend of u and we obtain a singular solution. The optimal control is described as:

$$\frac{\partial H_c}{\partial u} \begin{Bmatrix} > 0 \\ = 0 \\ < 0 \end{Bmatrix} \Rightarrow u^* = \begin{Bmatrix} u_{max} \\ \text{undetermined} \\ 0 \end{Bmatrix} \tag{18}$$

where

$$\sigma = \frac{\partial H_c}{\partial u} = -\lambda_c - \frac{\partial R}{\partial u} = -\lambda_c - \frac{2\pi x p_R}{k}. \tag{19}$$

If there is a singular solution ($\sigma = 0$) u^* ($0 < u^* < u_B$), equation (19) indicates that the marginal benefit of reducing the size of the invasion (λ_c) must equal the marginal costs that led to such reduction. If there is no singular solution, the optimal control contains only the extreme levels of control and there will be as many switches (from $u^* = u_{max}$ to $u^* = 0$ or *vice versa*) as the number of roots that σ has.

Applying the conditions of the maximum principle we identified (see Appendix 1) five critical points in time determining the optimal control path: τ, the optimal time to switch policy (solution of the unconstrained problem); t_{erad}, the time when the invasion is eradicated (constraint (16) is binding); t_{xmax} the time when all the susceptible range is invaded (constraint (17) is binding); and the starting ($t = 0$) and

final time T of the time horizon. τ is obtained by solving for t in equation (20) when $\sigma = 0$:

$$\sigma = \frac{1}{k} 2\pi \left(-p_R \left(ct - tu_{max} + x_0 \right) + \frac{\Psi}{r^2} - \frac{1}{r^2} e^{r(t-T)} \Psi \right) \tag{20}$$

where:

$$\Psi = c \left(D^* + D^* rt \right) + p_R r u_{max} - D^* \left(u_{max} + rtu_{max} - rx_0 \right)$$

and σ has only one root.

t_{erad} and t_{xmax} are obtained by solving for t in equation (21) when $x = 0$ and $x = x_{max}$ respectively:

$$x = \left(c - u_{max} \right) t + x_0 \tag{21}$$

It is not possible to check for singular solutions analytically. We employed numerical methods instead to check that σ does not vanish for a positive interval of time. We ruled out singular solutions and the optimal control was considered a normal bang-bang control (Lewis and Syrmos, 1995). We can summarise the different type of optimal control policies into five scenarios (assuming that we initially control, then accept the invasion rather than accepting first, then controlling the invasion):

$$\begin{bmatrix} \text{Case A} \\ \text{Case B} \\ \text{Case C} \\ \text{Case D} \\ \text{Case E} \end{bmatrix} \begin{bmatrix} 0 < \tau < (t_{erad}, \, t_{xmax}, T) \\ 0 < T < (\tau, \, t_{erad}, \, t_{xmax}) \\ 0 < t_{xmax} \leq (\tau, \, T) \\ 0 < t_{erad} \leq (\tau, \, T) \\ (\tau, \, t_{erad}, \, t_{xmax}) < 0 < T \end{bmatrix} \Rightarrow \begin{bmatrix} u^* = u_{max} \\ u^* = u_{max} \\ u^* = u_{max} \\ u^* = u_{max} \\ u = 0 \end{bmatrix} \text{for} \begin{bmatrix} 0 \leq t \leq \tau \\ 0 \leq t \leq T \\ 0 \leq t \leq t_{xmax} \\ 0 \leq t \leq t_{erad} \\ 0 \leq t \leq T \end{bmatrix} \text{and} \{ u^* = 0 \} \text{ for}$$

$$\begin{Bmatrix} \tau < t < T \\ - \\ t_{xmax} < t < T \\ t_{erad} < t < T \\ - \end{Bmatrix} \tag{22}$$

The type of optimal control policies are: Case A where $u = u_{max}$ until $t = \tau$; after that we accept the invasion that will continue spreading. In case B, we control the invasion during the entire time period and not all the susceptible area is occupied. In case C, we control the invasion until the entire susceptible area is occupied and then we accept it. In case D, the control is applied until eradication is achieved; then control stops. In case E, we accept the invasion without any attempt to control it.

Model parameterisation

We estimated p_R from the eradication campaign against CPB in 1976-77 in Thanet (Kent, UK) where a colony occupied an area of 184m^2 within a 19ha field. This campaign involved the following activities within a radius of 1.6 km: several aircraft and terrestrial insecticide spraying, compensation to farmers for the destruction of crops, use of bait crops and multiple inspections by Ministry officers (Bartlett, 1980). We assumed a homogeneous distribution of potato production through the landscape. The total costs of removal, (in 2005 pounds) added up to £102070 (119.21 £/km^2 of landscape treated, Table 1). On the other hand, the unit cost due to damages of an invaded ha of potato (D^*) add up to 53.54 £/ha (Waage *et al*., 2005). These include costs due to inspection, insecticide application, yield losses and export losses. We expressed those costs per km^2 of landscape (to match with the units of the predictions of the R-D model). The asymptotic velocity of spread (*c*) was estimated using equation (2) (values of parameters in Table 1). Given that potato and other *Solanum* species are very widespread in the UK, we assumed that in all the areas where there where adequate climatic conditions for the development of CPB, *Solanum* species were present. The maximum radius for the four main scenarios considered (circular or semicircular invasion under current climate conditions and climate change projections) was estimated assuming a circle and semicircle of equivalent area to the area of the susceptible range for CPB in the UK (79500 km^2 for temperatures from 1960-90 and 160700 km^2 for climate change projections for 2060-70) (Baker, *et al*., 1996). In addition, we assumed that the plant protection agency would be able to deploy control outlays so as to maintain a maximum spread velocity reduction of 10 km/year (u_{max}).

Results

In many cases, eradication is the only option considered by government agencies unless the invasion is too large, in which case acceptance is the policy option adopted. There is a need to know when to attempt eradication and if there are other policies like slowing down the invasion that are optimal before the final acceptance of the invasion. For all parameters combinations, the optimal policy corresponded to some form of control after discovery and then acceptance. As expected, it was never optimal to accept first the invasion and then control for it after the switching point.

Effect of initial size of invasion and agency's maximum spread velocity reduction capability on the type of optimal policy

The model identified eradication policies against CPB in the UK as optimal for low initial infestation sizes and for high agency's maximum spread velocity reduction capability (u_{max}) (Figure 2). On the other hand, for agencies incapable of deploying an invasion size reducing campaign, it was not optimal to accept CPB without adopting a slowing down policy for a period of time before the final acceptance of the invasion (Figure 2). The required u_{max} that makes eradication optimal increased with increasing initial sizes of invasion. For instance, an initial invasion of 30 km (75 km) radius would need at least an u_{max} of 5 km/year (7 km/year) for eradication to be optimal (Figure 2).

Effect of the unit cost ratio and the spread velocity on the type of optimal policy

Whereas for the case of CPB a policy of acceptance without control was not optimal, that policy would be optimal for other IAS presenting a lower unit cost ratio (D^*/p_R) (Figure 3). That is, IAS that are very costly to remove and at the same time do not inflict relevant damage costs per unit of invaded area (costs ratio < 0.04), should be left to spread naturally, independently of their spread velocity. On the other hand, slow spreading invaders (up to 2.5 km/year) should be eradicated independently of their unit cost ratio (as long as cost ratio > 0.04 and u_{max} = 10 km/year). For spread velocities below u_{max} it was optimal to control until a switching point and then to accept the invasion. The time at which the switch occurred was closer to the starting

point of the time horizon with decreasing unit cost ratios. For higher unit cost ratios and IAS spreading faster than u_{max}, control efforts should occur for the entire time horizon (Figure 3).

Effects of climate change, introduction point and spread velocity

The effect of climate change implied larger susceptible ranges of invasion. This had no effect at low spread velocities (3.1 km/year) because the total susceptible range was not occupied (Table 2). By contrast, when higher spread velocities (50 km/year for historical spread rates) led to total susceptible range occupation within the time horizon, the size range and shape of the invasion had an effect on the total overall cost, type of optimal policy and switching point (compare columns 3rd and 4th to 7th and 8th in Table 2).

Effect of u_{max} on total overall costs and total removal costs

u_{max} had a large effect on the success of the optimal management policy (Figure 4a). The total overall costs due to the invasion were a decreasing function of u_{max}, indicating the importance of being able to carry out large and effective campaigns through time. The peak of total costs of removal occurred for u_{max} close to and below the invasion spread (Figure 4b). That is, it is optimal to control for long periods of time if we are capable to slow spread considerably. On the other hand, if u_{max} is very low, acceptance occurs at an early stage resulting in less total costs of removal. Equally, if u_{max} is high, we will achieve eradication soon and the total costs of removal are also lower (Figure 4b).

Effect of spread velocity on total overall costs and total control costs

The total overall costs are an increasing function of spread velocity (Figure 5a). Total control costs are also an increasing function of spread velocity until spread velocity is considerably greater than the u_{max} (by 6 km/year, Figure 5b). The reason for this is that for high speed velocities, total invasion and acceptance (both make $u^* = 0$) occur earlier in the time horizon, leading to a decrease in total removal costs.

Sensitivity analysis

The sensitivity analysis confirmed the findings described above: the switching point occurred closer to the beginning of the time horizon for high u_{max} and closer to the end of the time horizon for higher initial invasion sizes and spread velocities (Figure 6a); and the total overall costs increased for higher initial invasion sizes, damage unit cost and velocity of the invader and were reduced for high u_{max} (Figure 6b).

Discussion

We have presented a simple, yet general, bioeconomic model to identify the switching points for the management of a spreading invasion using barrier zones. In previous work on this problem the Euler equation was employed (Sharov, 2004, Sharov and Liebhold, 1998). We have used optimal control theory instead, which has the advantage of considering explicitly the relationship between the control variable and the state of the system (Chiang, 1992). In order to solve the optimal control problem, we needed to establish the relationships between total removal costs, size of invasion and total damage costs. Several empirical forms relating control and damage exist (Lichtenberg and Zilberman, 1986). We chose those forms that provided a realistic description of the system whilst being as simple as possible. We assumed a linear relationship between the aimed spread velocity reduction and total costs of removal and between the aimed spread velocity reduction and the reduction of spread velocity. We assumed also a linear relationship between invasion size and total damage costs. The choice of relationships influences the type of solution obtained. In our case, we obtained a normal bang-bang solution (an example of a bang-bang solution in the control of the spreading of plant diseases is found in Forster and Gilligan, 2007). This indicates that it is optimum to spend either all resources on control or no resources at all. We identified the switching point between maximum control and zero control, i.e. the point at which any sort of control campaigns should end. In addition, since the state variable (invasion size) was constrained, we identified two other points in time at which control efforts should also cease: the time of eradication and the time at which all the susceptible range is occupied. These points in time, together with the starting and final points of the time horizon, shape the optimal control policy. Knowing the critical switching points, we developed policy plots that can be used as preliminary decision making tools in order to gauge the optimal policy given the ecological and economic parameters of the invader and the ecosystem.

In the case of the potential Colorado potato beetle invasion in the UK, the optimal policy for different combinations of model parameters confirmed previous findings in the literature: Eradication was optimal for low initial sizes of invasion (Sharov, 2004) and when there was a high agency's maximum spread velocity reduction capability (u_{max}) (Figure 2). High u_{max} also led to lower total overall costs of invasion (Figure 4a)

(Cacho *et al*., 2008; Hall and Hastings, 2007; Taylor, 2004). Eradication was also preferred for low velocity of spread of the invader (Cacho, *et al*., 2008) provided the ratio of unit cost of damage and removal per unit of area was not very low (Figure 3) (Forster and Gilligan, 2007). Very low unit cost ratios made acceptance of the invasion without attempt to control it the optimal policy (independently of the spread velocity of the invader, Figure 3). Surprisingly, eradication was not always the optimum policy even with sufficient outlays to carry it out (Figure 3). For the majority of parameter combinations a policy switch happened within the time horizon, showing how, even if eradication was not feasible, slowing down the spread until a certain point in time was optimal (Sharov and Liebhold, 1998).

We assumed in the model that the government agency was fully aware of the initial size of invasion upon discovery and of the effectiveness of the control measures over the invasion size. Whereas this deterministic approach allows us to clearly identify the trade-offs between parameters, the model would improve if these parameters were depicted by uncertainty distributions and the problem solved using stochastic optimization (Olson and Roy, 2005). The introduction of stochasticity is left, tantalisingly, for future research. Population dynamics and dispersal processes are also affected by stochasticity and Allee effects (Dennis, 2002), especially at low population densities. We considered our approach reasonable since we focused on already established and spreading organisms.

R-D models tend to underestimate the spread of organisms performing long distance dispersal events (LDDE) (Andow *et al*., 1990). Since CPB can perform LDDE assisted by weather events, R-D models might underestimate its dispersal in the UK. Alternative spread models that account for LDDE could be incorporated in the analytical model at the cost of increasing the complexity of the analytical analysis (e.g. stratified diffusion models (Shigesada *et al*., 1995) and integro-difference models (Kot *et al*., 1996)). This approach was regarded as beyond the scope of this study.

The assumption of constant u_{max} presented the advantages of analytical tractability and ease of interpretation (i.e. if the agency can maintain $u_{max} > c$ (spread velocity), the invasion size will be reduced). A constant u_{max} implies increasing (decreasing) total costs of removal with increasing (decreasing) invasion size. In reality, the agency

will increase control efforts if the management measures are perceived as effective, i.e. if a reduction of the invasion is achieved. In the same way, if initial control efforts appear to be ineffective, they start to be gradually decreased.

The introduction of further non-linearities in the model could be considered. For instance, Burnett *et al*., (2007) assumed increasing unit costs of removal with decreasing sizes of invasion due to greater searching efforts. We judged that in our case, the increase in the costs of trapping efforts for small population densities will not be relevant enough as to justify making the unit cost of removal dependent on the size of the invasion. In contrast, this is reasonable in their case, since the accessibility to certain areas of the archipelago of Hawaii played an influential role on the searching costs. In another instance, Sharov and Liebhold (1998) assumed that a convex function would better explain the relationship between invasion size and total costs of removal, by reflecting that big invasions would require the use of less effective and hence marginally more costly control measures. In our case, we argue that the invasion by CPB is not likely to exhaust the control resources of the plant protection agency and hence the assumption of constant unit costs of removal would be adequate.

Further improvements could be brought about by relaxing the assumption of an homogeneous landscape. This could be achieved by adopting a spatially explicit simulation approach. In this case, more flexible spread models like metapopulation models (e.g. see an applications to bioeconomics by Brown and Roughgarden, (1997)), cellular automata or individual based models (e.g. Breukers *et al*., 2006) could be considered.

In this paper, a bioeconomic model to estimate the optimal policy and switching point of invasion management campaigns was presented. This model represents a useful tool for preliminary exploration of the optimal policy given a set of biological and economic parameters. The integration of the dispersal patterns of the invader in the bioeconomic modelling of IAS invasions is strongly recommended, as demonstrated by this model. This integration will help us to estimate more precisely the time periods during which we should apply the brake to IAS invasions, which can bring about a greater measure of efficiency of control over these invasions.

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Appendix 1: Application of Pontryagin maximum principle

We need to determine the roots in the switching function σ. In this case, the sign of σ depends on the costate variable λ_c. We proceed to investigate the form of λ_c. Applying equations (8) and (9) to equation (14) in the text we obtain:

$$\frac{\partial \lambda_c}{\partial t} = \frac{2D^* \pi x}{k} + \frac{2\pi p_R u}{k} + r\lambda_c . \tag{1a}$$

We evaluate the state and a costate solution in the case the optimal path equals u_{max} for all t. We initially attempt to solve the problem as an unconstrained problem ignoring the constraint in the state variable (equations (16) and (17)).

Since u is constant and equal to u_{max} we can integrate (13) and apply the boundary condition (15) to obtain:

$$x = \left(c - u_{max}\right)t + x_0 \tag{2a}$$

Substituting (2a) into (1a) and setting $u = u_{max}$, we can solve (1a) as an ordinary differential equation:

$$\lambda_c[t] = \frac{1}{kr^2} 2\pi \left(-c\left(D^* + D^* rt\right) - p_R r u_{max} + D^* \left(u_{max} + rt u_{max} - rx_0\right) \right) + ae^{rt} \tag{3a}$$

Where a is an integration constant that is defined by applying the boundary condition (15) to (3a). Rearranging terms we obtain:

$$\lambda_c[t] = \frac{1}{kr^2} 2e^{-rT} \left(e^{rt} - e^{rT}\right) \pi \left(c\left(D^* + D^* rt\right) + p_R r u_{max} - D^* \left(u_{max} + rt u_{max} - rx_0\right)\right)$$
$$\tag{4a}$$

Thus, substituting (2a) and (4a) into (18) and rearranging terms, the expression of σ results:

$$\sigma = \frac{1}{k} 2\pi \left(-p_R \left(ct - t u_{max} + x_0\right) + \frac{\Psi}{r^2} - \frac{1}{r^2} e^{r(t-T)} \Psi \right) \tag{5a}$$

Where:

$$\Psi = c\left(D^* + D^* rt\right) + p_R r u_{max} - D^* \left(u_{max} + rt u_{max} - rx_0\right)$$

The switching points $t = \tau_i$ are obtained by equating (24) to zero and solving for t. Unfortunately, τ_i cannot be obtained from (24) by algebraic methods. We employed numerical methods instead.

The switching point τ corresponds to the solution of the unconstrained problem. Taking into account the constraints of x in equations (16) and (17) implies that if τ is greater than the time at which $x = 0$ (eradication occurs at $t = t_{erad}$) or $x = x_{max}$ (total invasion occurs at $t = t_{xmax}$) (we obtain t_{erad} and t_{xmax} by solving equation (2a) setting x $= 0$ and x $= x_{max}$ respectively), that solution occurs outside the permissible region. Then the constraint of the state variable (either equation (16) or (17)) becomes binding and by complementary slackness:

$$(u - c) = 0$$

Since, by definition, $c = 0$ when $x = 0$ or $x = x_{max}$, u has to be zero as well.

Tables and figures

Table 1. Parameters of the model.

Symbol	Description	Value	Source
x_0	Radius of initial size of invasion (km)	20	Assumed
u_{max}	Agency's maximum spread velocity reduction capability (km/year)	10	Assumed
p_R	Unit cost of removal (£/km^2)	119.21	Estimated (Bartlett, 1980)
D	Diffusivity (km^2/year)	60	(Waage et al., 2005)
ε	Intrinsic growth rate	0.04	Estimated (Yasar and Gungor, 2005)
c	Asymptotic velocity (km/year)	3.10	Estimated using Equation (2)
C_h	Historical spread Europe (km/year)	50	(Follett, et al., 1996)
B	Budget for control (£1000/year)	150	Assumed
D^*	Unit cost of damage (£/km^2)	50.29	(Waage et al., 2005)
r	Discount rate	0.06	Assumed
x_{maxA}	Maximum radius, circular invasion, current climate (km)	159.07	Estimated (Baker et al., 1996).
x_{maxB}	Maximum radius, semicircular invasion, current climate (km)	224.97	Estimated (Baker et al., 1996).
x_{maxC}	Maximum radius, circular invasion, climate change (km)	226.17	Estimated (Baker et al., 1996).
x_{maxD}	Maximum radius, semicircular invasion, climate change (km)	319.85	Estimated (Baker et al., 1996).
T	Time horizon	20	Assumed
A_{potato}	Area of potato grown in England and Wales (1000 ha)	142	Average from 2004 to 2008 (DEFRA, 2007).

Table 2. Effect of climate change, introduction point and spread velocity on Colorado potato beetle optimal control policy in the UK. Eight scenarios are considered according to the climate projection: current climate and climate change; the establishment point: centre of the susceptible range (centre) and near the coast (coast); and the annual dispersal velocity of the invasion: predicted from the reaction-diffusion model (c = 3.1 km/year); and assumed from historical spread rates in Europe (c = 50 km/year). The net prevent value (NVP) of costs reported are: R(x,u), total costs of removal; D(x) total damage costs caused by the remaining invasion; total of overall costs (Total costs); switching time from management to acceptance and the type of switch: τ, optimal time to stop control efforts; t_{erad}, time at which eradication occurs; t_{xmax} time at which all the susceptible range is invaded; and the type of optimal control policy (policy). Costs values are expressed in £ millions and switching time in years. The rest of parameters of the model present the values in Table 1.

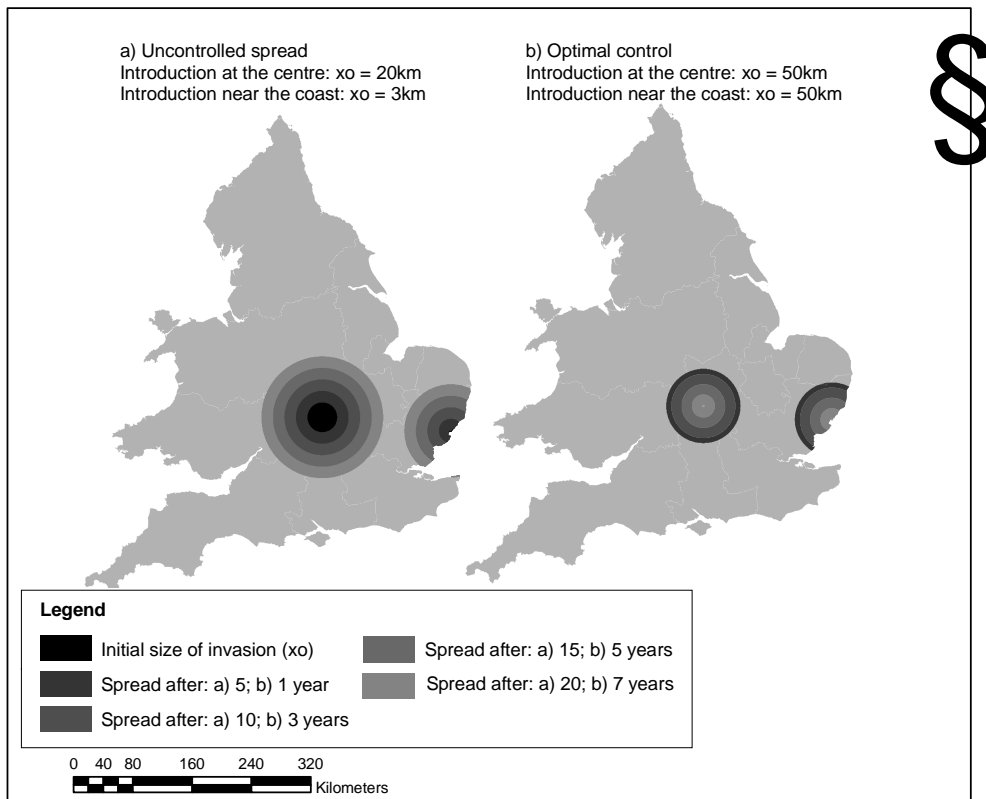| Climate	Current climate scenario				Climate change scenario			
c	3.1		50		3.1		50	
Introduction	centre	coast	centre	coast	centre	coast	centre	coast
R(x,u)	0.134	0.067	1.090	0.545	0.134	0.067	1.090	1.519
D(x)	0.031	0.015	40.095	20.047	0.031	0.015	74.625	64.610
Total costs	0.164	0.082	41.185	20.592	0.164	0.082	75.716	66.130
Switch time	3	3	2	2	3	3	2	4
Switch type	t_{erad}	t_{erad}	t_{xmax}	τ	t_{erad}	t_{erad}	τ	τ

Figure 1. Illustrative maps of the model predictions for the invasion by CPB in the UK after potential establishment in the centre of the susceptible range and near the east coast. a) Natural spread without control: the invasion expands its range continuously. b) Optimal control: the range of the invader is reduced due to a moving barrier zone. Eradication occurs at the 8th year after discovery. The parameters used by the model are those of Table 1.
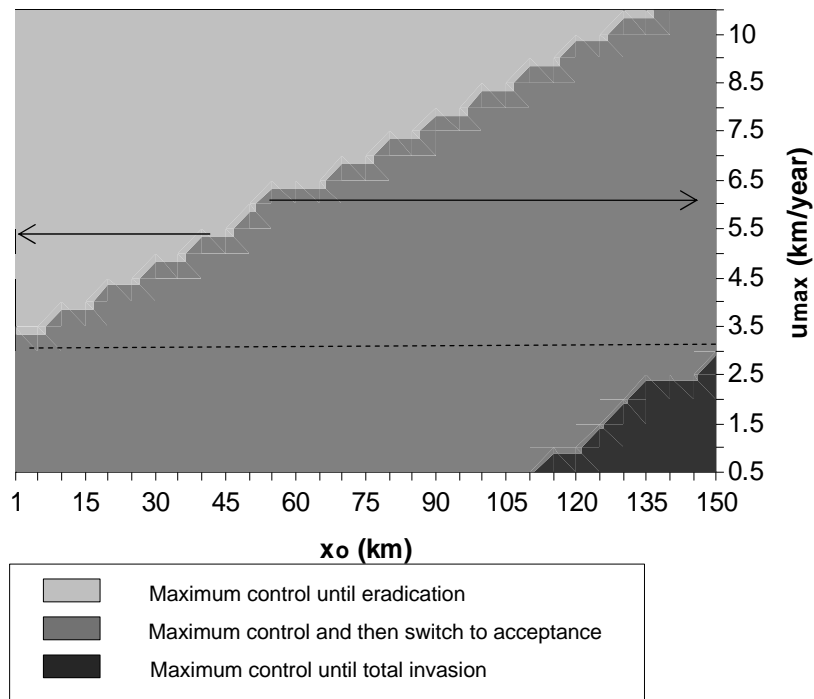
Figure 2. Policy plot of the optimal policy option for different radius of initial sizes of invasion (x_0) and agency's maximum spread velocity reduction capability (u_{max}) for the case of invasion by Colorado potato beetle in the UK. Below (above) the dashed line: u_{max} < CPB spread velocity (u_{max} > CPB spread velocity). The arrows indicate the progression of the size of the invasion under the optimal path. The rest of the values were kept fixed at the values in Table 1.
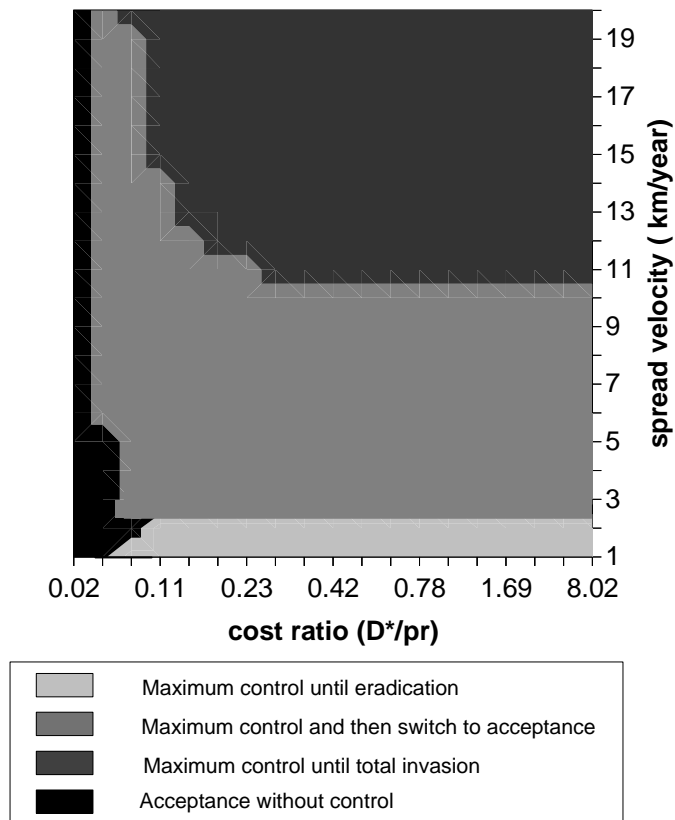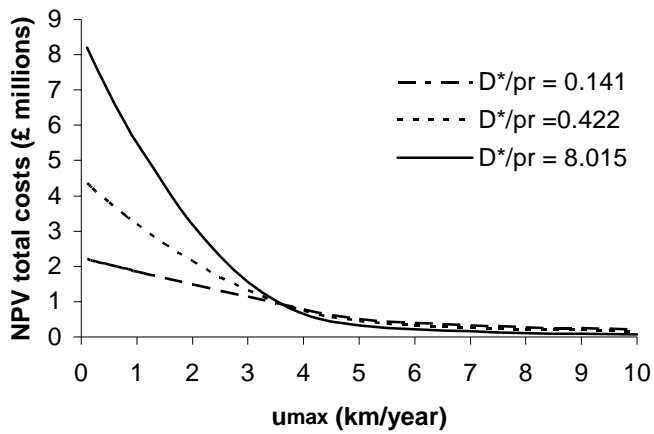
Figure 3. Policy plot of the optimal policy option depending on the unit cost ratio: unit cost of damage (D^*)/ unit cost of removal (p_R) and the asymptotic spread velocity of the invader (c). The rest of the parameters present the values in Table 1.
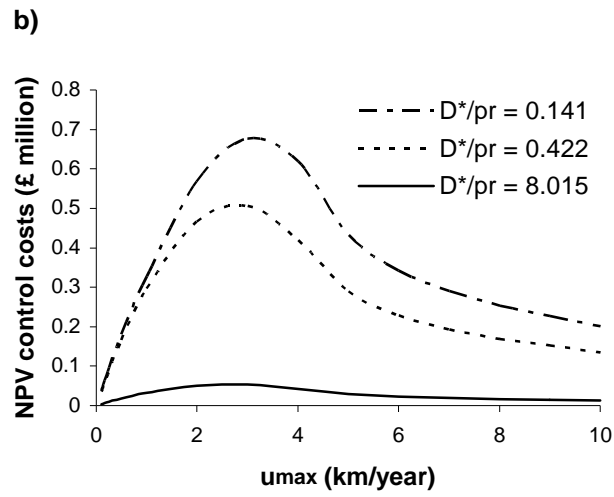
b)

Figure 4. Net present value (NPV) of the total overall costs due to the invasion (a) and NPV of the total costs of removal (b) for different agency's maximum spread velocity reduction capability (u_{max}). Three levels of unit cost ratios (unit cost of damage, D^*/ unit cost of removal, p_R) were considered.
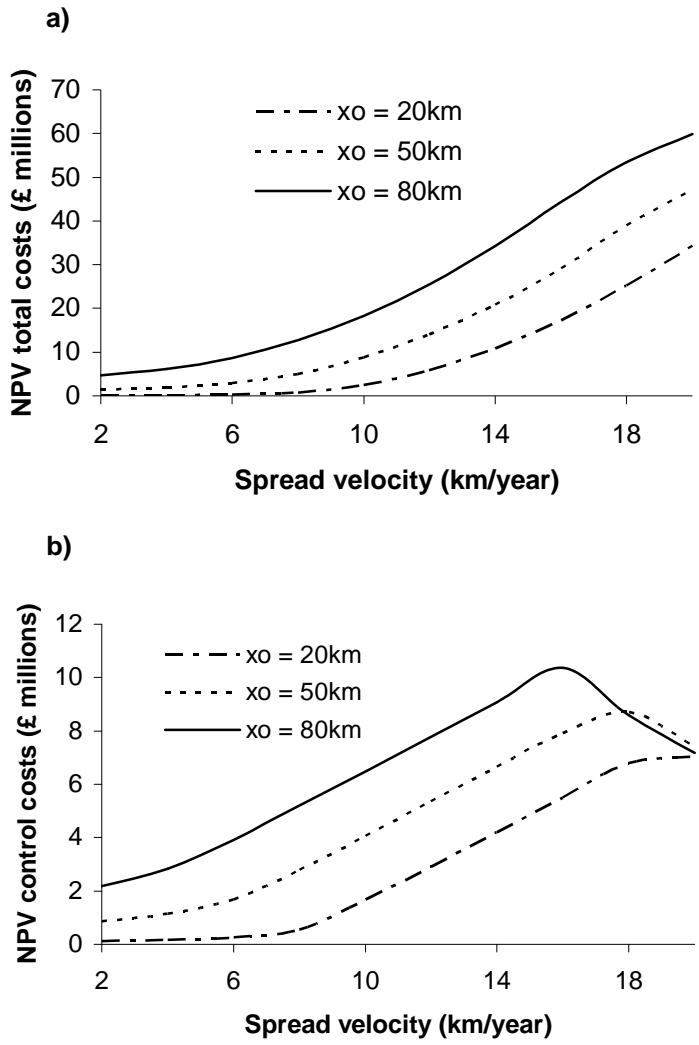
a)

b)

Figure 5. Net present value (NPV) of the total overall costs due to the invasion (a) and NPV of the total costs of removal for different invader spread velocity. Three levels of initial size of invasion (xo) were considered.
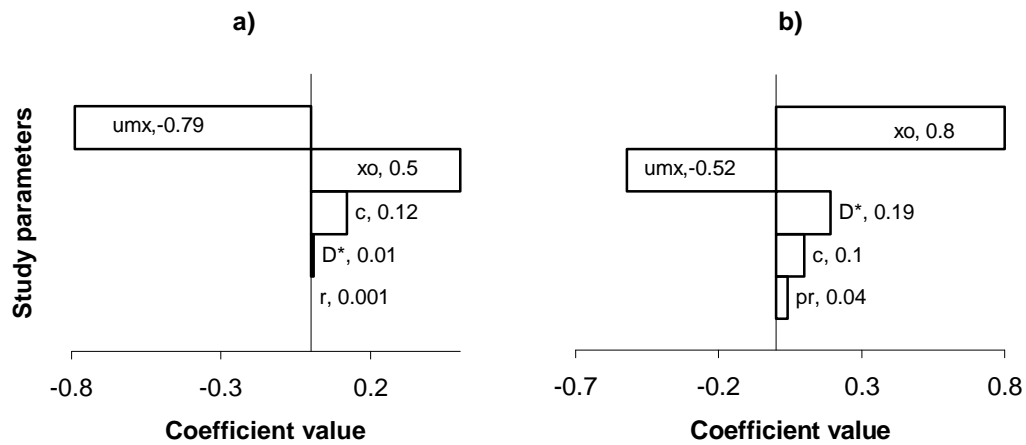
Figure 6. Sensitivity analysis of the optimal control model outputs to model parameters using a tornado chart. The outputs are: a) optimal time to stop invasion control efforts and; b) net present value of total overall costs due to the invasion. Model parameters were sampled from a uniform distribution with a maximum (minimum) of +50% (-50%) the original values of the model parameters using Monte Carlo simulation with Latin Hypercube sampling (see table 1 for the initial value of the parameters and their description). The values in the chart are the Spearman's rank correlation coefficients relating the sampled model parameters values and the outputs. umx : agency's maximum spread velocity reduction capability; xo: initial invasion size; c: spread velocity; D^*: unit cost of damage; r: discount rate; and p_R: unit cost of removal.