Ecological Economics 69 (2010) 1303–1312

Contents lists available at ScienceDirect

Ecological Economics

journal homepage: www.elsevier.com/locate/ecolecon

Methods

Comprehensive bioeconomic modelling of multiple harmful non-indigenous species

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ARTICLE INFO

Article history:
Received 29 July 2009
Received in revised form 28 January 2010
Accepted 2 February 2010
Available online 24 February 2010

Keywords:
Biosecurity
Genetic algorithm
Invasive alien species
Optimal control
Propagule pressure

ABSTRACT

Harmful non-indigenous species (NIS) introductions lead to loss of biodiversity and serious economic impacts. Government agencies have to decide on the allocation of limited resources to manage the risk posed by multiple NIS. Bioeconomic modelling has focused on single species and little is known about the optimal management of multiple NIS using a common budget. A comprehensive bioeconomic model that considers the exclusion, detection and control of multiple NIS spreading by stratified dispersal and presenting Allee effects was developed and applied to manage the simultaneous risk posed by Colorado beetle, the bacterium causing potato ring rot and western corn rootworm in the UK. A genetic algorithm was used to study the optimal management under uncertainty. Optimal control methods were used to interpret and verify the genetic algorithm solutions. The results show that government agencies should allocate less exclusion and more control resources to NIS characterised by Allee effects, low rate of satellite colonies generation and that present low propagule pressure. The prioritisation of NIS representative of potential NIS assemblages increases management efficiency. The adoption of management measures based on the risk analysis of a single NIS might not correspond to the optimal allocation of resources when other NIS share a common limited budget. Comprehensive bioeconomic modelling of multiple NIS where Allee effects and stratified dispersal are considered leads to a more cost-effective allocation of limited resources for the management of NIS invasions.

1. Introduction

Government agencies need to manage multiple harmful non-indigenous species (NIS) introductions to avoid losses to biodiversity and serious economic impacts on agriculture, fisheries, forestry and industry (OTA, 1993). Quantitative models aimed at identifying the economically optimal strategy to manage NIS should combine the disciplines of invasion ecology and economics (Leung et al., 2002) that hitherto have tended to remain separate. NIS spread and management has been successfully captured by biological invasion spread theory (good reviews are Hastings, 1996; Higgins and Richardson, 1996) and applied ecology models (e.g. Moody and Mack, 1988; Taylor and Hastings, 2004). Surprisingly, these advances have not quite been integrated within the economic modelling of NIS management (Liebhold and Tobin, 2008). Aspects commonly overlooked by the economic literature of NIS invasions management are: (i) long-distance dispersal events that are known to be very relevant to the rate of the invasion spread (Bossenbroek et al., 2007); and (ii) the importance of Allee effects (reduced survival probability in low population density colonies due for instance to the difficulty to find a mating partner, satiate predators or inbreeding depression) and propagule pressure on the establishment of isolated new colonies (Liebhold and Bascompte, 2003).

Recent bioeconomic models combining both ecology and economics for the management of single NIS have been insightful in determining the optimal management of NIS invasions (a good review is provided by Olson, 2006). Studies have focused on the exclusion of NIS related to trade (e.g. Costello and McAusland, 2003; Horan et al., 2002), prevention or control of a single NIS (e.g. Buhle et al., 2005; Carrasco et al., 2010; Eiswerth and Johnson, 2002; Olson and Roy, 2002) and more recently an integrative approach to study the trade-off between control and prevention has been adopted (e.g. Burnett et al., 2008; Finnoff et al., 2007; Kim et al., 2006; Olson and Roy, 2005; Perrings, 2005). Regarding the methodologies used to solve the dynamic optimization problem of NIS management, different approaches have been used: models where optimal control theory is employed (Burnett et al., 2008; Eiswerth and Johnson, 2002; Kim et al., 2006, 2007; Olson and Roy, 2005) stochastic dynamic programming applications (Eiswerth and van Kooten, 2007; Leung et al., 2002; Shoemaker, 1981) and genetic algorithms (Taylor and Hastings, 2004).

Despite these advances, little is known about the economically optimal management of multiple NIS coming from different pathways and regions with a limited budget, because modelling efforts have focused mainly on a single NIS or pathway (but see Kim et al., 2007

Abbreviations: CB, Colorado beetle; NIS, harmful non-indigenous species; NPV, net present value; PRR, potato ring rot; WCR, western corn rootworm.

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doi:10.1016/j.ecolecon.2010.02.001

which focuses on multiple regions and is the basic work from which the analytical exploration builds). This focus on a single NIS overlooks the fact that in most cases NIS management activities share a common and limited national budget. For this reason, it is necessary to develop more comprehensive models that integrate the management of multiple NIS under uncertainty.

Allee effects and propagule pressure are fundamental factors that determine the potential success of a biological invasion (Leung et al., 2004; Liebhold and Tobin, 2008). Although they are important concepts in the field of invasion ecology, they have received very little attention in the economic modelling of NIS. An exception is the work by Burnett et al. (2008) that assumes strong Allee effects and uses a minimum population threshold before which an invasive population of tree snakes cannot start growing in Hawaii. In this paper, the literature of economic modelling of NIS management is advanced by including Allee effects and propagule pressure explicitly in the economic analysis.

Here a comprehensive bioeconomic model that integrates exclusion, detection and control of multiple NIS is developed. The model is used to study the influence of Allee effects, propagule pressure and stratified dispersal of a certain NIS on the optimal economic allocation of exclusion and control efforts among multiple NIS. It is also used to test the cost-effectiveness of agencies carrying out risk analysis on individual NIS that are representative of pathways that might carry assemblages of multiple unknown NIS.

The problem is first approached using optimal control theory (Pontryagin maximum principle) (Pontryagin et al., 1962; Sethi and Thompson, 2000) to explore the necessary optimal management conditions (Appendix A). Then, uncertainty is introduced into the parameters and the model is applied for the case study of the potential invasion by the NIS western corn rootworm (WCR), Colorado potato beetle (CB) and the bacterium *Clavibacter michiganensis* subsp. *sepedonicus* responsible of the disease potato ring rot (PRR) in the UK (see the electronic supplementary material for a description of the case studies). The optimal control problem was solved using a genetic algorithm combined with Monte Carlo simulation.

2. Methods

2.1. The Model

The stages of a NIS invasion are divided into entry, establishment and spread. The management measures available to the government agency to manage NIS i are the control variables of the problem: exclusion (Ex_i) that attempts to decrease the probability of entry and establishment; detection before discovery (Sb_i) that aims to discover the invasion at its early stages; and control (Q_i) that can be aimed at eradicating the invasion, containing it or slowing it down and encompasses removal and surveillance after discovery. Here we define C_{Exi}, C_{Sbi} and C_{Qi} as the total expenditure on exclusion, detection before discovery and control of NIS i.

2.1.1. Entry and Exclusion

Let the annual probability of entry and establishment of the first colony by NIS i be p_i^{inv}. We model the process of a successful entry and first establishment per year using a Poisson stochastic process (Vose, 1997):

$$f_i^{inv} = \left[\exp\left(-p_i^{inv}\right)\right]\left(p_i^{inv}\right) \tag{1}$$

where f^{inv} is the probability density function of successful entry and establishment. We assume that $p'_{inv}<0$ and $p''_{inv}>0$, where the prime denotes the derivative with respect to C_{Ex}, i.e. the probability of invasion of the NIS is inversely proportional to the government expenditure on the NIS exclusion with decreasing marginal returns. We model the relationship between probability of invasion and exclusion as (modifying Leung et al., 2005):

$$p_i^{inv} = \frac{p_{ri}}{1+\theta_i C_{Ex_i}} \tag{2}$$

where p_{ri} is the probability of invasion when no efforts at exclusion are in place and θ_i is the effectiveness in reducing the probability of invasion per monetary unit spent on exclusion measures on NIS i.

2.1.2. Detection Before Discovery

Once the NIS has entered and established, official control measures are not started unless the NIS is discovered. The conditional probability of discovery at time t, given non-discovery up to time t is modelled as a hazard function. The hazard is explained by the covariates C_{Sbi} and A_{ti} (area invaded at time t). A Cox proportional hazards model (Cox, 1972) was employed:

$$\lambda\left(t_k; C_{Sb_i}; A_{ti}\right) = \lambda_{0i}(t)\exp\left(\beta_{1i}C_{Sb_i} + \beta_{2i}A_{ti}\right) \tag{3}$$

where t_k is the time of discovery of the invasion k; λ_o is the baseline hazard function defined at the mean of the explanatory variables; β_j are the regression coefficients. C_{Sbi} and A_t have an effect on the baseline hazard function shifting it up or down.

2.1.3. Stratified Dispersal and Establishment

A successful invasion event leads to an initial main colony that grows following a reaction–diffusion model (Skellman, 1951) by which the radius increases at a constant radial velocity $v_i = 2(\varepsilon_i d_i)^{1/2}$ in a circular fashion where ε_i is the intrinsic growth rate and d_i is the diffusion constant of the NIS i. The main colony generates a propagule pressure (N) due to propagules arriving at the same location in the same time period after performing long-distance dispersal. New entries after the current invasion has been discovered become new satellite colonies with probability equal to $A_t/A_{\max}$ where $A_{\max}$ is the total susceptible range of the NIS. Long-distance dispersing propagules might generate satellite colonies ("nascent foci"). The probability of establishment of a propagule to generate a new colony (p_e) is modelled with a Weibull distribution (Dennis, 2002; Leung et al., 2004):

$$p_{ei} = 1 - \left(\exp(-\alpha_i N_i)^{\gamma i}\right) \tag{4}$$

where α_i equals to $-\ln(1-\eta_i)$ and η_i is the probability of establishment of a single migrating individual that is assumed equal to the density of the host in the landscape. γ_i is a shape parameter that reflects the severity of Allee effects on NIS i. When $\gamma_i = 1$, there is no Allee effects. Once established, the nascent foci grow following also a reaction–diffusion model. A scattered colony model where nascent foci do not coalesce with other colonies was employed (Shigesada et al., 1995). The original main colony and the nascent foci produce new propagules at a rate ρ_i. The number of propagules (n_{prop}) is assumed proportional to the area of the colony (A_{col}): $n_{\text{prop}}(t) = \rho_i A_{\text{col}}(t)$ (Shigesada et al., 1995). The agency prioritises the control of nascent foci and uses the remaining funds for control for the management of the original colony (Moody and Mack, 1988).

2.1.4. Control After Discovery: Surveillance and Removal

Control costs are composed of surveillance costs after discovery and removal costs. The agency is uncertain about the extent of the invasion and needs to perform surveillance activities to gain knowledge of the areas invaded, i.e. for a unit of invaded area to be removed it has to be detected first. The marginal cost of control (c') is expressed as (modifying Burnett et al., 2007):

$$c' = \frac{dC_{Q_i}}{dQ_i} = (c_R + c_{\text{det}})A_{\text{det}}$$

where c_{det} is the unit cost of detection of an invaded unit of area and A_{det} is the area where the NIS has been detected at time t; and c_R is the unit cost of removal. The agency will allocate resources to surveillance activities until the cost of removal of the amount of invaded area detected equals the remaining funds available in the budget for control activities.

Surveillance activities follow diminishing marginal returns with the size of the invasion. This represents the greater difficulty to eradicate the last proportions of area invaded with respect to the initial proportions (Myers et al., 1998):

$$c_{\text{det}} = c_S + \frac{c_{\text{det}-\max} - c_S}{1 + A_t}$$

where c_s is the unit cost of surveying a unit of susceptible area; $c_{\text{det}-\max}$ is the cost of detecting the last invaded unit of area. It is assumed that: $c_{\text{det}-\max} = c_s{\cdot}A_0$ where A_0 is the size of the area invaded when control activities started against the invasion.

2.1.5. Damages

The NIS invasion generates damages D_t where $D_t = D^* A_t$ and D^* is the unit cost of damage caused by the NIS per unit of area invaded. D^* can present the following relationships with the area invaded: (a) linear relationship where $D^* = D_0^*$ where D_0^* is constant; (b) convex relationship where $D^* = D_0^* + (A_t/b_1)^2$; (c) concave relationship where $D^* = D_0^* + (A_t/b_2)^{1/2}$. Case (a) is the default case used in the numerical simulation–optimization experiments.

2.1.6. The Policy Problem of the Agency

The problem of the agency is to allocate resources on exclusion, detection before discovery and control among N potential NIS to minimise the net present value (NPV) of the total costs due to the invasions and their management. Expressed in a generic way:

$$\begin{aligned} Minimize: \int_0^T e^{-r\cdot t}\Bigg\{\sum_{i=1}^{N} \Bigg(& F_{inv\ i}F_{di}\Big[C_{Qi}(Q_i, A_{ti}) + D_i(A_{ti}) + C_{Exi} + C_{Sb_i}\Big] \\ & + F_{inv\ i}(1-F_{di})\Big[D_i(A_{ti}) + C_{Exi} + C_{Sb_i}\Big] + (1-F_{inv\ i})\Big[C_{Exi} + C_{Sb_i}\Big]\Bigg)\Bigg\}dt \end{aligned} \tag{5}$$

where r is the discount rate, T is the time horizon, $F_{inv\ i}$ and F_{di} are the cumulative probability functions of successful initial invasion and discovery of the NIS i at time t. The minimisation is subject to a budget constraint on the management activities, the dynamics of entry and first establishment, spread and discovery of each NIS. Optimal control theory (Pontryagin, 1962; Sethi and Thompson, 2000) was used to explore analytically the behaviour of the control variables in their optimal paths (Appendix A). A genetic algorithm was used to obtain the optimal control paths for the presented empirical formulation of the problem.

2.2. Model Parameterisation

A panel of expert pest risk analysts was asked to provide estimates of entry and establishment probability given different levels of exclusion efforts and the time till discovery given sizes of the initial invasion and levels of detection for WCR, CB and PRR (see electronic supplementary material). The models were fitted to the data using survival analysis and nonlinear regression methods in the R environment (R Development Core Team, 2005).

2.3. Simulation and Optimization: Genetic Algorithms

The optimal time path of the control variables under uncertainty was obtained using a genetic algorithm. Genetic algorithms are a numerical optimization method inspired from evolutionary biology and used to find solutions to complex problems with poorly understood solution spaces (Holland, 1975). Genetic algorithms have extensively been used in the fields of engineering, economics and biology (Axelrod, 1984; Chen, 2002; Dawid, 1999). For instance genetic algorithms have been used to solve the travelling salesman problem, large scheduling problems, portfolio optimization and engineering problems like the design of bridge structures (Dawid, 1999). However their use in the area of bioeconomics of NIS control is very rare (see as an exception Taylor and Hastings, 2004). In a genetic algorithm, a computer simulation is performed where a population of abstract representations of candidate solutions of the optimization problem (chromosomes) evolves to better solutions according to a fitness criterion (Goldberg, 1989). In our case, the functioning of the genetic algorithm expressed in programming pseudocode was:

1. Generate an initial population of 500 chromosomes (each chromosome contains the levels of detection, exclusion and control for each NIS and year, i.e. “genes”).
2. The model is run for each chromosome using Monte Carlo simulation with Latin Hypercube sampling until convergence of the estimate of the mean of the distribution of NPV of the total costs (our fitness criterion).
3. Select the fittest chromosomes (those that led to lowest mean NPV of total costs).
4. Create “offspring” chromosomes through: (i) a crossover function that interchanges the genetic material of the fittest chromosomes and (ii) a mutation function that performs random changes in a proportion of the “genes” of the chromosomes to allow for exploration of new regions of the solution space.
5. Replace the least-fit chromosomes of the population with the fitter offspring chromosomes.
6. The genetic algorithm continues creating new offspring chromosomes until the mean NPV of total costs is not reduced by more than 0.01% for the last 5000 generated chromosomes (visual inspection confirmed the convergence of the algorithm to a stable optimal solution).

Genetic algorithms have been used to solve complex optimal control problems where, as in our case, sufficiency conditions of optimality cannot be applied analytically (Seywald et al., 1995; Yamashita and Shima, 1997). Whereas their probabilistic nature does not allow them to find with certainty the exact global minimum, it prevents them from being contained by local minima unlike hill-climbing optimization methods (Mardle et al., 2000). In this respect, mutation processes are essential to avoid a premature convergence to local minima because they ensure a good coverage of the solution space (Dawid, 1999), allowing genetic algorithms to obtain a good approximation of the global minimum. Their probabilistic nature allows them also to handle constrained optimization problems and find boundary solutions with less difficulty than hill-climbing methods. The main problem with constraints is how to deal with candidate solutions that violate the constraints. For these cases fitness penalty functions or rejection rules are employed. In our case, a rejection rule that discarded the chromosomes that violated the problem constraints was used.

Discretization of the optimal control problem to a yearly time-step was necessary in order to apply the genetic algorithm (Seywald et al., 1995; Yamashita and Shima, 1997) i.e. discretization of the time, exclusion, control and detection efforts. Uncertainty distributions of the model parameters were introduced (Table 1). The software RiskOptimizer (Palisade-Corporation, 2006) was employed. We set the rate of crossover and mutation at 0.5 and 0.1 respectively (Palisade-Corporation, 2006). There is a trade-off between the precision of the solution obtained (length of the chromosome) and the speed of convergence to an optimal solution. We limited the values of the control variables to 10% fractions of the annual budget and assumed that management policies could only be changed every two years in a twenty year time horizon ($(9^{10})^{(20/2)} = 2.656{\cdot}10^{95}$ possible solutions).

Table 1
Uncertainty distributions of the parameters of the model. The parameters regarding entry, establishment and time till discovery were elicited from expert information (electronic supplementary material). p_R: baseline probability of entry; Θ: cost-effectiveness of exclusion efforts; β_1 and β_2 are the effect of detection efforts and area of the invasion on the time to discovery; ρ: rate of satellite generation; ε: intrinsic growth rate; d: diffusivity (km^2/year); c_R: unit cost of control (£/km^2); D^*: unit cost of impacts (£/km^2); η: probability of establishment of a satellite colony; γ: shape parameter reflecting the severity of Allee effects; c_S = unit cost of surveillance activities; b_1 and b_2: scale parameter of the convex and concave damage functions. U denotes uniform distribution. The "assemblage" column presents the uncertainty distributions sampled to generate the NIS assembled with CB (see Fig. 4).

Parameter	WCR	CB	PRR	Assemblage
p_R	U(0.27,0.74)[c]	U(0.22,0.34)[c]	U(1.1E−03, 0.054)[c]	U(0,1)
Θ	U(1.7E−06, 5.3E−05)[c]	U(2.0E−05, 4.4E−05)[c]	U(2.5E−06, 4.6E−06)[c]	–
β_1	4.34E−07[c]	0	2.93E−06[c]	U(0, 1E−06)
β_2	1.35E−05[c]	8.11E−06[c]	9.84E−06[c]	U(1E−05, 1E−06)
ρ	Pert(0.36, 0.72, 1.08)[c]	Pert(0.2, 0.4, 0.6)[c]	Pert(0.1, 0.2, 0.3)[c]	U(0,1)
ε	Pert(1, 2, 3)	Pert(0, 0.025, 0.05)[b]	Pert(3, 5, 7)[b]	U(0,7)
d	Pert(12, 23, 35)[c]	Pert(50, 60, 70)[b]	Pert(0, 0.025, 0.05)	U(0,70)
c_R	Pert(80, 163, 240)[c]	Pert(40, 119, 200)[a]	Pert(41, 68, 134)[c]	U(40,240)
D^*	Pert(60, 120, 180)	Pert(0, 50, 100)[b]	Pert(354, 726, 1114)[b]	U(0,1200)
η	0.008	0.0094	0.0094	U(0.008,0.0094)
γ	U(1,2)	U(1,2)	1	U(1,2)
c_s	18.054[c]	8.512[c]	14.235[c]	U(8,18)
b_1	22,035	32,140	45,000	–
b_2	88	160	229	–
Common annual budget for management of all NIS			£8,000,000	
Number of NIS in the assemblage			U(0,30)	

Sources: [a]estimated from (Bartlett, 1980); [b](Waage et al., 2005); [c]electronic supplementary material.

3. Results

3.1. Analytical Exploration: Condition of Equimarginality

Assuming an interior solution, the maximum principle (Pontryagin, 1962; Sethi and Thompson, 2000) was used to derive the following necessary optimality conditions of the problem (Appendix A):

$$\begin{aligned}(-F_{inv\ i}F_{di}-\lambda_1)\frac{\partial C_{Qi}}{\partial Q_i}+\lambda_{i2}\frac{\partial Z_i}{\partial Q_i}\\ =(-F_{inv\ i}F_{di}-F_{inv\ i}(1-F_{di})-(1-F_{inv\ i})-\lambda_1)\frac{\partial C_{Exi}}{\partial Ex_i}+\lambda_{i3}\frac{\partial \Phi_i}{\partial Ex_i}\\ =(-F_{inv\ i}(1-F_{di})-(1-F_{inv\ i})-\lambda_1)\frac{\partial C_{Sbi}}{\partial Sb_i}+\lambda_{i4}\frac{\partial \Psi_i}{\partial Sb_i}=0\end{aligned} \tag{6}$$

where λ_1 is the Lagrangian multiplier associated to the budget constraint; λ_{i2}, λ_{i3}, λ_{i4} are costate variables (reflecting the shadow price) and Z, Φ, and Ψ are partial time derivatives of the variables area invaded, probability of entry and first establishment and probability of discovery respectively.

Condition (6) determines that for a dynamic allocation of the budget among the different NIS and management activities to be economically optimal, the marginal avoided costs due to the NIS obtained by each management activity should equal the marginal costs of such activity. This type of condition is called an *equimarginal* condition and the marginal costs and marginal avoided costs due to the NIS can differ between each NIS and management activity (Kim et al., 2007).

Relaxing the assumption of interior solution, i.e. state and control constraints can be binding, the optimal path presents modifications of the equimarginal condition. When a certain NIS i is eradicated or totally invades its susceptible range, management efforts towards NIS i become zero and the ratio of marginal costs and marginal benefits of the control of NIS i (Q_i) drops from the equimarginal condition until a new introduction of NIS i takes place (see Appendix A).

Regarding the budget inequality constraint, the Kuhn–Tucker conditions are given by:

$$\lambda_1\geq 0;\ B-\sum_{i=1}^{N}\left(C_{Ex_i}+C_{Sb_i}+C_{Q_i}\right)\geq 0;\ \lambda_1\left(B-\sum_{i=1}^{N}\left(C_{Ex_i}+C_{Sb_i}+C_{Q_i}\right)\right)=0.$$

By complementary slackness, the budget constraint will be binding ($\lambda_1>0$) whenever the total expenditure on the management of the group of NIS equals the budget (B). The budget constraint creates a competitive interaction between different management options and NIS, i.e. focusing on the exclusion of one NIS implies that fewer resources are available for the management of the other NIS. If the budget is not a limiting factor for the management of all NIS, i.e. the budget constraint is not binding ($\lambda_1=0$) the solution of the optimal control problem is equivalent to the independent solution of the optimal control problem for each individual NIS. Due to the complexity of the problem, (λ_1 is a function of the level of exclusion, detection and control of each NIS), explicit expressions for the path of λ_1 and the control variables as a function of time could not be found analytically. We used instead numerical methods to study the optimal paths of the control variables. The simulation–optimization algorithm was applied to the concrete case of WCR, CB and PRR and allowed to study the general case when control and state constraints are binding.

3.2. Optimal Paths Obtained Using Numerical Methods

In the baseline scenario, the allocation of management resources pointed towards the condition of equimarginality. WCR was allocated a large share of the management resources (£23.8 million on exclusion and £30.1 million on control, Fig. 1(a) "baseline scenario") because its likelihood of entry, establishment and spread velocity is higher than those of CB and PRR. This makes the potential avoided costs due to WCR management very high and grants a large allocation of the management resources for WCR.

In contrast, economic impacts were not so relevant for the final allocation of management resources. For instance, PRR that presented clearly the highest potential economic impacts (Table 1) was not allocated as much resources as WCR because of its low probability of entry and establishment and slow spread (Fig. 1(a)). This indicates that the overall costs are more sensitive to the biological characteristics of the NIS than to its economic damage characteristics.

The optimal paths for WCR, CB and PRR (Fig. 1(b), (c) and (d)) showed that the management measures presented cyclic fluctuations. These cycles corresponded to the mean time of entry and eradication of each NIS invasion in the time horizon. For instance, control of PRR (Q-PRR, Fig. 1(d)) remains as zero after one peak (eradication achieved) until a new invasion event occurs. Other results are that, as expected, more resources were allocated to the exclusion of the NIS at

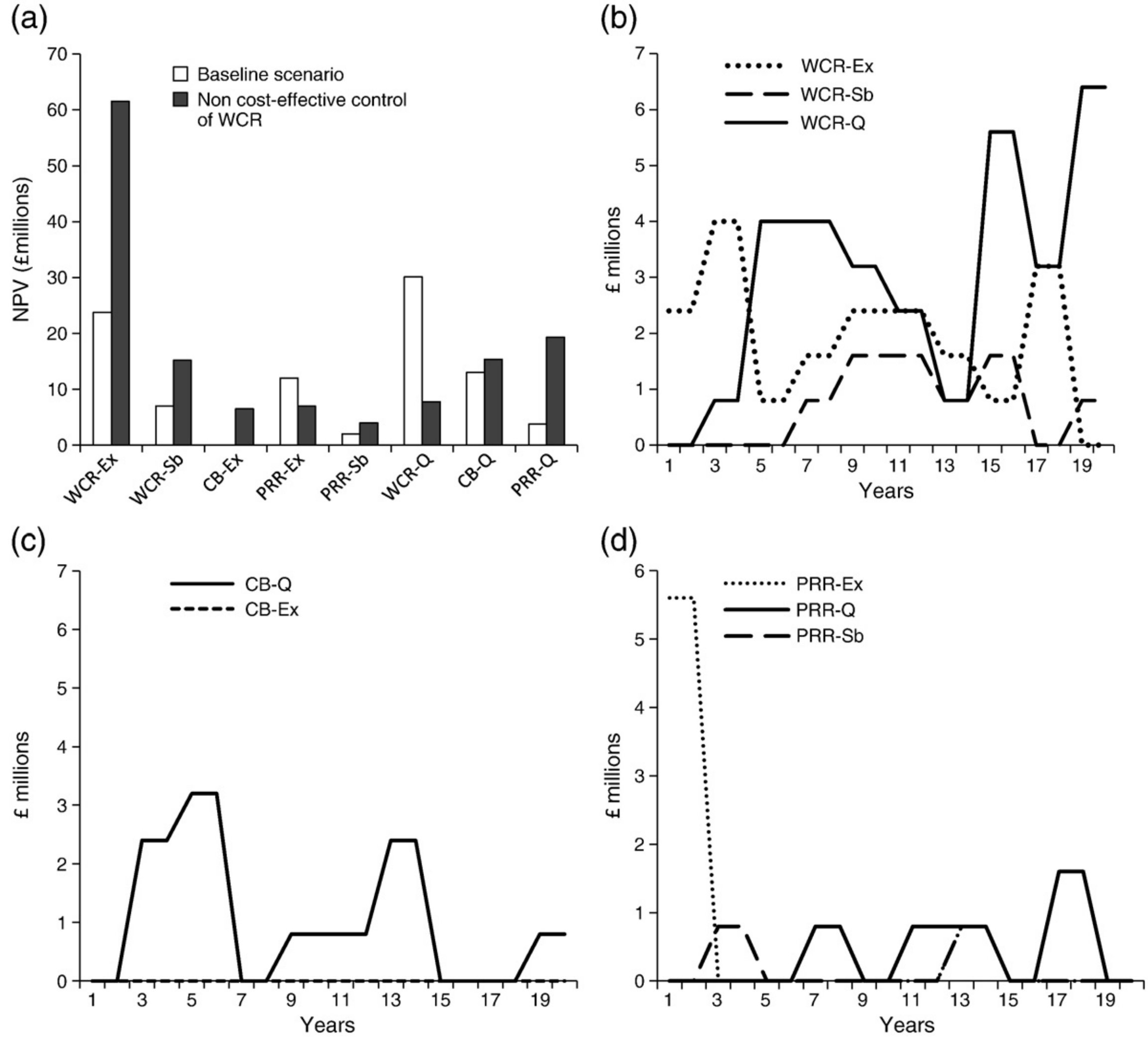

Fig. 1. (a) Optimal allocation of management resources for the exclusion, detection and control of, CB, PRR and WCR in the UK. The "baseline scenario" corresponds to the parameter values of Table 1. In the "non cost-effective control of WCR" scenario, the unit cost of control of WCR was increased ten times. Ex: exclusion; Sb: search before discovery; Q: control (removal and surveillance after discovery). (b), (c) and (d) expenditure in the optimal control paths on exclusion, detection and control of WCR, CB and PRR respectively.

the beginning of the time horizon, i.e. control is only relevant once the NIS is established (Fig. 1(b) and (d)) and non cost-effective management measures (relative to other alternative options) might remain at zero for the entire time horizon (e.g. exclusion of CB in the "baseline scenario", Fig. 1(c)). A further simulation experiment was used to test the condition of equimarginality: the unit cost of WCR control was increased ten times (Fig. 1, "non cost-effective control of WCR"). As a result, outlays previously allocated for control of WCR in the baseline scenario (£30.1 million) were reduced to £7.8 million and used instead for the detection before discovery of WCR that increased from £7 to 15.2 million and exclusion of WCR that increased from £23.8 to 61.5 million. The increase of the unit cost of control of WCR also affected the optimal allocation of resources to other NIS. For instance, the resources for control of PRR increased from £3.7 to 19.3 million and the exclusion of CB from £0 to 6.5 million. This is because these management options became relatively more cost-effective under the new scenario. It would not have been possible to estimate these inter-NIS effects with a risk analysis that focused on a single NIS.

3.3. The Effect of Satellite Generation and Propagule Pressure

Higher rates of satellite colonies generation and higher propagule pressure had a relatively similar effect: greater management efforts were allocated to exclusion and fewer to post-discovery control (Fig. 2(a) and (b)). The reason was that NIS that presented a high propagule pressure (high probability of establishment of satellite colonies) and generated high number of new satellites, invaded their susceptible range very rapidly. These dispersal characteristics make control of such NIS ineffective, rendering exclusion as the only cost-effective alternative.

3.4. The Influence of Allee Effects on the Economically Optimal Management Mix

When some of the NIS in the pool of NIS considered presented Allee effects, the overall total costs generated decreased (Fig. 3(a)). The optimal mix of management efforts also varied towards allocating more post-discovery control and less exclusionary efforts for the NIS presenting high Allee effects (WCR in our simulation experiment, Fig. 3(b)). The reason was that the probability of establishment of new colonies was lower (leading to lower spread velocities). For this reason, it was more cost-effective to wait for a new invasion to start and then eradicate it rather than to attempt to exclude the NIS.

3.5. The Effect of Convexity and Concavity of the Damage Function

We employed convex and concave damage functions instead of a linear damage function. We varied the convexity and concavity

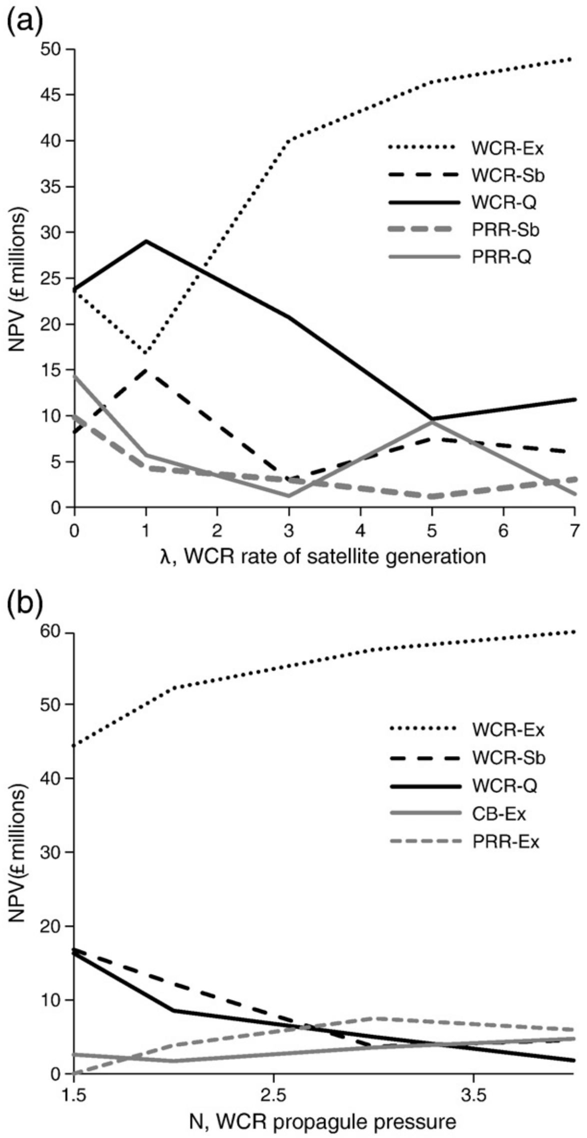

Fig. 2. (a) The effect of satellite generation and (b) the effect of propagule pressure on the optimal mix of management strategies. Expenditure on Ex: exclusion; Sb: search before discovery; Q: control (removal and surveillance after discovery).

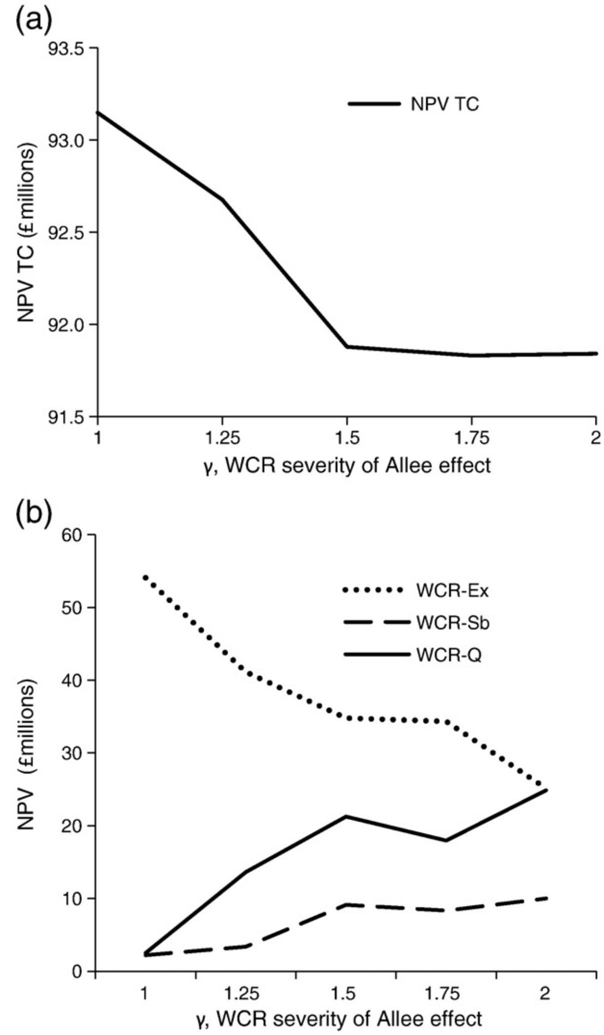

Fig. 3. The influence of Allee effects on the optimal management mix. (a) Mean net present value of total costs (NPV TC) as a function of Allee effects severity. (b) Decrease of exclusionary expenditure and increase of expenditure on control and search before discovery measures against WCR for increasing severity of Allee effects. Ex: exclusion; Sb: search before discovery; Q: control (removal and surveillance after discovery).

(b_1 from 22,035 to 4435 and b_2 from 88 to 44) for the case of WCR. No changes in the optimal mix of management allocation could be detected. The reason was that the optimal policy against WCR is one of eradication for small areas invaded; therefore the effect of the nonlinear damage function was not noticeable. The experiment was repeated in a situation where the optimal management of WCR corresponded to slowing down the invasion (we decreased the cost-effectiveness of exclusion of WCR from Uniform($1.7 \cdot 10^{-6}$, $5.3 \cdot 10^{-5}$) to $9.12 \cdot 10^{-7}$ and the unit cost of control from Pert(80, 163, 240) to $5.4 £/km^2$). In this case, a change from a linear damage function into an increasingly convex function led to an increasing allocation of resources for the control of WCR in an attempt to stop WCR from occupying its whole susceptible range.

3.6. Management of NIS Assemblages

The efficiency of considering risk analysis of NIS assemblages was evaluated. CB was assumed to be representative of a pathway carrying an uncertain number N of NIS of unknown biological and economic characteristics (Table 1). Because those NIS were assumed to share the pathway with CB, exclusion activities against CB were also effective in reducing the probability of entry of the NIS of the assemblage. The results showed that the consideration of assemblages led to a reduction of the overall costs (Fig. 4(b)). The NIS assemblage attracted more management resources (Fig. 4(a), high expenditure on exclusion of CB) with respect to an allocation that only considered the known NIS.

4. Discussion

Here we combined analytical methods with genetic algorithm simulation–optimization to solve a problem of multiple NIS exclusion, detection and control. This approach allowed us to increase the complexity of the economic analysis including common aspects of biological invasions: Allee effects, propagule pressure and stratified dispersal. The inclusion of these aspects led to new management insights.

Comprehensive bioeconomic models integrating prevention, control and detection are not common in the economic literature of NIS management. Focusing on the trade-off between prevention and control has tended to suppress the important distinction between detection and removal. Besides, studies centred on the trade-off

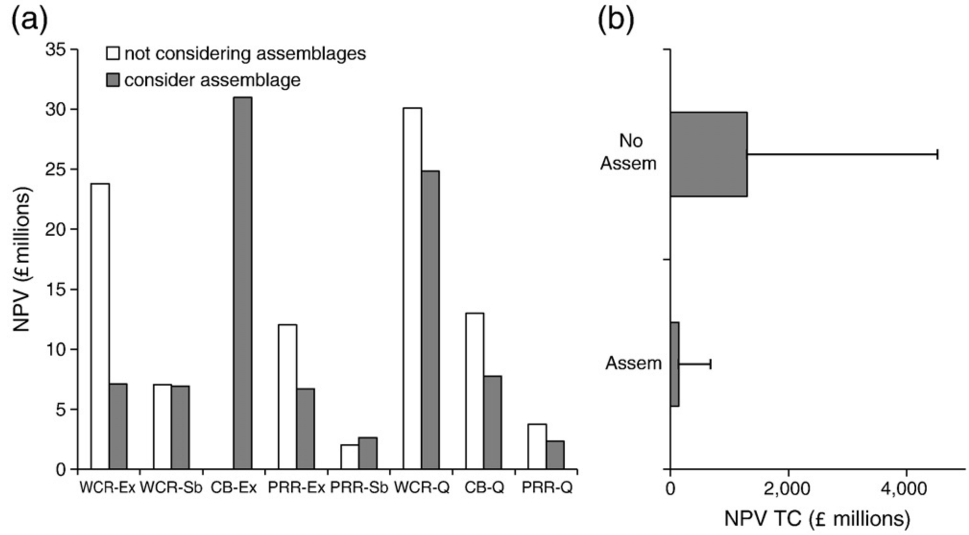

Fig. 4. (a) Optimal allocation of management resources for the exclusion, detection and control of, CB, PRR and WCR in the UK with and without considering hypothetical NIS assemblages. (b) Distribution of the net present value of total costs (NPV-TC) for a policy that consider potential assemblages ("Assem") and one that does not ("No Assem"). The bar indicates the 50th percentile and the error bars the 95th percentile. The "not considering assemblages" scenario represents the allocation of management resources attending to the known 3 NIS. In the "consider assemblage scenario" the government considers the uncertainty of potential assemblages in the pathway of CB (see Table 1 for the characteristics of the unknown NIS in the assemblage).

between detection and removal have not incorporated prevention simultaneously into the analysis. Given the importance of the establishment of the NIS and the role of early detection on the progression of the invasion, these aspects should be incorporated into bioeconomic models together with prevention and control. Further pursuit of this line of research by incorporating the factors that determine the risk of establishment into comprehensive bioeconomic models would be necessary.

Risk analysis based on single NIS might not lead to the optimal allocation of economic resources when a limited budget has to be allocated among several NIS. Consideration of other NIS that compete for budget allocations is necessary to estimate the optimal strategy. The results showed that complex interactions between the cost-effectiveness of alternative management measures and the NIS considered play an important role on the optimal final allocation of management resources. For instance, if the measures to manage a NIS that presents an unacceptable risk are very costly and ineffective, the agency will attain a more cost-effective allocation of economic resources if no action is adopted against such NIS and the resources are instead allocated to other NIS for which cost-effective management alternatives exist.

The results demonstrated that for the optimal strategy corresponding to exclusion, detection and control of multiple NIS to be estimated, it is necessary to take into account the biological characteristics of the NIS and the cost-effectiveness of the management measures available. Managing a group of NIS where some of them present Allee effects led to lower net present value of total costs (Fig. 3(a)). In the optimal allocation of management resources, more post-discovery control resources were allocated to the NIS that presented higher Allee effects. The reason was that Allee effects reduced the number of satellite colonies that would successfully establish, thus, reducing the spread velocity of the NIS and making it more cost-effective to control. In addition, resources shifted from control to exclusion of NIS with low or no Allee effects that presented stratified dispersal and high propagule pressure. The reason was that NIS with such characteristics are very difficult to control once established, i.e. the marginal avoided costs per unit of exclusion are very high whereas the marginal avoided costs per unit of post-discovery control are very low. Management decisions, however, should also be based on the cost-effectiveness of the options available. For instance, an explosive invader might have no Allee effects and be extremely costly to exclude but relatively easy to detect once established. In this case, campaigns for early detection instead of exclusion might be the optimal policy. Related to this example, detection before discovery was a relevant strategy in the form of short and intense campaigns separated in time in the case of PRR, which had a low probability of entry but could generate high economic impacts (Fig. 1(d)). These short campaigns helped to gain knowledge of a potential establishment of the NIS, increasing the probability of success of a rapid eradication intervention.

The consideration of NIS assemblages led to a greater allocation of management resources to those NIS representing an assemblage of NIS. The implications are that it might be more cost-effective to allocate more management resources to NIS representing pathways posing a high risk than to important single NIS not likely to belong to a pathway entailing high risk. Current agency practices choosing NIS representative of pathways carrying potential assemblages of NIS are thus adequate. This result is analogous to a firm that presents economies of scope, i.e. the average fixed costs of the firm are spread over a greater number of customers if more product lines are opened. In the case of considering potential assemblages, the fixed budget of the agency can be potentially spread over more NIS. As a result, there is a potential increase of the avoided economic impacts per fraction of the budget used.

The model could be developed further in a number of ways: (i) spatially explicit models could be used to explore the influence of landscape connectivity and colonies coalescence on the optimal allocation of management resources for multiple NIS; (ii) ecological interactions between the potential NIS could be considered, e.g. predator–prey interactions; (iii) alternative methods that could bring insight into the economic modelling of multiple NIS management are neural networks. Their potential has recently been shown with the use of self-organising maps to prioritise the management of different NIS according to their risk of invasion (Worner and Gevrey, 2006).

We employed both linear and nonlinear damage functions in the bioeconomic model (Sharov and Liebhold, 1998; Olson and Roy, 2005). The choice of the type of function might affect the optimal policy, especially when management could influence the final extent of the area invaded. Linear functions are adequate if the economic impact per unit of area invaded can be approximated as constant and the NIS spreads in a relatively homogeneous landscape. However, a nonlinear relationship will be more adequate when increasing marginal damages to the industry are seen with an increasing number of firms affected; as a few firms affected would not result in a serious impact to the industry, but more firms affected could cause entire industries to be impacted. Nonlinear functions would also be preferred if the NIS invades progressively the habitat patches of a native species that exhibits metapopulation dynamics (Parker, 1999).

4.1. Conclusions

Whereas individual risk analysis for single NIS might suffice for the management of single NIS when management resources are not limited, our results demonstrate the necessity to use comprehensive bioeconomic models for the optimal management of multiple NIS when national biosecurity budgets are limited and have to be allocated among multiple NIS. The consideration of the biological characteristics of the NIS was shown to be essential for an adequate allocation of resources, especially regarding Allee effects, propagule pressure and long-distance dispersal mechanisms. Comprehensive bioeconomic models of multiple NIS will provide agencies with powerful tools to better allocate management resources, identify the necessary management adjustments when considering NIS assemblages and assess objectively a range of alternative policy options.

Acknowledgements

We thank the panel of experts for their collaboration in the parameterisation of the model and two anonymous referees for their comments that greatly improved the paper. The research was funded by a grant of the UK Department for Environment, Food and Rural Affairs (DEFRA) (NB 53 9005) and the Rural Economy and Land Use Program (RES-229-25-0005). The views expressed herein are exclusively our own and do not represent the views of DEFRA.

Appendix A

Analytical exploration: application of the Pontryagin maximum principle to a generic continuous formulation of the problem.

The problem of the government agency is to allocate resources on exclusion (Ex_{it}), detection before discovery (Sb_{it}) and control (Q_{it}) among N potential invasions by NIS$_i$ in order to minimise the net present value (NPV) of the total costs due to the invasions and their management:

$$\int_0^T e^{-r\cdot t}\left\{\sum_{i=1}^{N}\left(F_{inv\ i}F_{di}\left[C_{Qi}(Q_i,A_{ti})+D_i(A_{ti})+C_{Exi}+C_{Sb_i}\right]\right.\right.$$
$$\left.\left.+F_{inv\ i}(1-F_{di})\left[D_i(A_{ti})+C_{Exi}+C_{Sb_i}\right]+(1-F_{inv\ i})\left[C_{Exi}+C_{Sb_i}\right]\right)\right\}\mathrm{d}t \quad [A.1]$$

Subject to:

$$\sum_{i=1}^{N}\left(C_{Ex_i}+C_{Sb_i}+C_{Q_i}\right)\le B \quad [A.2]$$

$$\frac{\partial A_{ti}}{\partial t}=Z(\theta_i,Q) \quad [A.3]$$

$$\frac{\partial F_{inv\ i}(t)}{\partial t}=f_{inv\ i}(t)=\Phi(Ex_{it}) \quad [A.4]$$

$$\frac{\partial F_{di}(t)}{\partial t}=f_{di}(t)=\Psi(A_{ti},S_{bi}) \quad [A.5]$$

$$0\le A_{ti}\le A_{\max i} \qquad 0\le Ex_i,\ Q_i,\ Sb_i. \quad [A.6]$$

Eq. (A.1) represents the NPV of the total costs where: r is the discount rate; T is the time horizon; F_{inv} and F_d are respectively the cumulative probability function of successful initial invasion and discovery of the NIS at time t; C_Q, C_{Ex}, and C_{Sb} are respectively the cost functions of control, exclusion and detection efforts; A_{ti} is the invaded area at time t by NIS i; D_i are the costs caused by the NIS i in the area invaded. Ex_{it}, Sb_{it} and Q_{it} are called control variables and F_{inv}, F_d and A_t are called the state variables in an optimal control context. Eq. (A.1) reflects the expected costs of the potential states of nature: proportion of successful invasions that are discovered and treated; successful invasions that spread undetected; and successful exclusions of the NIS. Eq. (A.2) establishes that the sum of the costs of exclusion, detection and control for all NIS has to be less or equal than the annual budget (B). Eq. (A.3) is the equation of motion of the size of the invasion and represents the spread of the NIS$_i$ that depends on the biological parameters of the NIS and the control activities. Eqs. (A.4) and (A.5) are the equations of motion for the probabilities of successful invasion and discovery of the invasion. Z, Φ and Ψ denote functions relating the equations of motion with control variables and parameters. Eq. (A.6) is a constraint on the size of the invasion reflecting that the maximum susceptible range of invasion is limited.

The problem is an optimal control problem with three control variables (Ex_{it}, Sb_{it} and Q_{it}) and three state variables (A_{ti}, F_{inv} and F_d). The current value Lagrangian–Hamiltonian is:

$$LH=\left\{\sum_{i=1}^{N}\left(-F_{inv\ i}F_{di}\left[C_{Qi}(Q_i,A_{ti})+D_i(A_{ti})+C_{Exi}+C_{Sbi}\right]\right.\right.$$
$$\left.\left.-F_{inv\ i}(1-F_{di})[D_i(A_{ti})+C_{Exi}+C_{Sbi}]-(1-F_{inv\ i})([C_{Exi}+C_{Sbi}]\right)\right\}$$
$$+\lambda_1\left(B-\sum_{i=1}^{N}\left(C_{Exi}+C_{Sbi}+C_{Qi}\right)\right)+\lambda_{i2}(Z(\theta_i,Q))$$
$$+\lambda_{i3}(\Phi(Ex_it))+\lambda_{i4}(\Psi(A_{ti},S_{bi}))+\eta_{1i}(t)\cdot[Z_i(\theta_i,Q_i)]$$
$$-\eta_{2i}(t)\cdot[Z_i(\theta_i,Q_i)] \quad [A.7]$$

where λ_1 is the Lagrangian multiplier and λ_{i2}, λ_{i3}, λ_{i4} are costate variables. The necessary conditions for optimality are (Pontryagin et al., 1962; Sethi and Thompson, 2000):

$$\frac{\partial LH}{\partial Q_i}=(-F_{inv\ i}F_{di}-\lambda_1)\frac{\partial C_{Qi}}{\partial Q_i}+\lambda_{i2}\frac{\partial Z_i}{\partial Q_i}\le 0;\ Q_i\ge 0;\ Q_i\frac{\partial LH}{\partial Q_i}=0 \quad [A.8]$$

$$\frac{\partial LH}{\partial Ex_i}=(-F_{inv\ i}F_{di}-F_{inv\ i}(1-F_{di})-(1-F_{inv\ i})-\lambda_1)\frac{\partial C_{Exi}}{\partial Ex_i}$$
$$+\lambda_{i3}\frac{\partial\Phi_i}{\partial Ex_i}\le 0;\ Ex_i\ge 0;\ \ Ex_i\frac{\partial LH}{\partial Ex_i}=0 \quad [A.9]$$

$$\frac{\partial LH}{\partial Sb_i}=(-F_{inv\ i}(1-F_{di})-(1-F_{inv\ i})-\lambda_1)\frac{\partial C_{Sbi}}{\partial Sb_i}$$
$$+\lambda_{i4}\frac{\partial\Psi_i}{\partial Sb_i}\le 0;\ Sb_i\ge 0;\ Sb_i\frac{\partial LH}{\partial Sb_i}=0 \quad [A.10]$$

$$\frac{\partial LH}{\partial\lambda_1}=\left(B-\sum_{i=1}^{N}\left(C_{Ex_i}+C_{Sb_i}+C_{Q_i}\right)\right)\ge 0;\ B-\sum_{i=1}^{N}\left(C_{Ex_i}+C_{Sb_i}+C_{Q_i}\right)$$
$$\ge 0;\ \lambda_1\ge 0;\ \ \lambda_1\left(B-\sum_{i=1}^{N}\left(C_{Ex_i}+C_{Sb_i}+C_{Q_i}\right)\right)=0 \quad [A.11]$$

$$\frac{\mathrm{d}A_t}{\mathrm{d}t}=\frac{\partial LH}{\partial\lambda_{i2}}=Z(\theta_i,Q) \quad [A.12]$$

$$\frac{\mathrm{d}F_{inv}}{\mathrm{d}t}=\frac{\partial LH}{\partial\lambda_{i3}}=\Phi(Ex_{it}) \quad [A.13]$$

$$\frac{\mathrm{d}F_d}{\mathrm{d}t} = \frac{\partial LH}{\partial \lambda_{i4}} = \Psi(A_{ti}, S_{bi}) \qquad [A.14]$$

$$\frac{\partial \lambda_{i2}}{\partial t} = -\frac{\partial LH}{\partial A_{it}} + r\lambda_{i2} \qquad [A.15]$$

$$\frac{\partial \lambda_{i3}}{\partial t} = -\frac{\partial LH}{\partial F_{inv\ i}} + r\lambda_{i3} \qquad [A.16]$$

$$\frac{\partial \lambda_{i4}}{\partial t} = -\frac{\partial LH}{\partial F_{di}} + r\lambda_{i4} \qquad [A.17]$$

$$\lambda_{1i}(T)e^{rT} = 0;\ \lambda_{2i}(T)e^{rT} = 0;\ \lambda_{3i}(T)e^{rT} = 0;\ \lambda_{4i}(T)e^{rT} = 0 \qquad [A.18]$$

$$A_{ti}(T)\mathit{free};\ F_{inv\ i}(T)\mathit{free};\ F_{di}(T)\mathit{free} \qquad [A.19]$$

$$\begin{aligned}\frac{\partial LH}{\partial \eta_{1i}} &= Z_i(\theta_i, Q_i) \geq 0,\ \eta_{1i}(t)\cdot[Z_i(\theta_i, Q_i)] \geq 0,\ \eta_{1i}(t)\cdot[Z_i(\theta_i, Q_i)] \\ &= 0,\ A_{ti} \geq 0,\ \eta_{1i}(t)A_{ti} = 0,\ \left(\frac{\partial \eta_{1i}(t)}{\partial t} = 0 \text{ when constraint not binding}\right)\end{aligned} \qquad [A.20]$$

$$\begin{aligned}\frac{\partial LH}{\partial \eta_{2i}} &= Z_i(\theta_i, Q_i) \leq 0,\ \eta_{2i}(t)\cdot[Z_i(\theta_i, Q_i)] \leq 0,\ \eta_{2i}(t)\cdot[Z_i(\theta_i, Q_i)] \\ &= 0,\ A_{ti} \leq A_{\max i},\ \eta_{2i}(t)A_{ti} \\ &= 0,\ \left(\frac{\partial \eta_{2i}(t)}{\partial t} = 0 \text{ when constraint not binding}\right).\end{aligned} \qquad [A.21]$$

Eqs. (A.20) and (A.21) are the conditions due to the constrained state variable (Eq. (A.6)). The complementary-slackness conditions state that η_{1i} and η_{2i}, the Lagrangian multipliers, will be zero unless $A_{ti} = 0$ and $A_{ti} = A_{\max}$ respectively (the state constraints become binding).

Interior Solution

An interior solution occurs when the inequality constraint (A.6) is not binding for all t. In this case when all the control variables are greater than zero the Kuhn–Tucker conditions (A.8), (A.9) and (A.10) turn by complementary slackness into Eq. (6). Eq. (6) determines that for an allocation of the budget among the different NIS and management activities to be economically optimal, the avoided marginal costs due to invasion size reduction obtained by each management activity should equal the marginal costs of such activity for all NIS i. For instance, if MB_{11}/MC_{11} (the ratio between the marginal benefits and costs of management of NIS 1 with activity 1) is greater than MB_{23}/MC_{23} (management of NIS 2 with activity 3) it will be optimal to allocate more resources to activity 1 to manage NIS 1 until the equimarginal condition is reached. In reality the control activities can be zero, for instance before the NIS has been discovered, when NIS are explosive invaders very costly to control or the probability of entry is very low (e.g. PRR). The boundary solutions for the control variables are allowed by the Kuhn–Tucker conditions ((A.8), (A.9) and (A.10)) and were explored using the genetic algorithm.

Constraints in the State Variables Binding

When constraint (A.6) becomes binding for the area of some NIS (eradication or total invasion by a certain NIS) Eqs. (A.20) and (A.21) become necessary. They correspond to the indirect adjoining method (Sethi and Thompson, 2000). Eqs. (A.20) and (A.21) indicate that for $A_i = 0$ and $A_i = A_{\max i}$, by complementary slackness Z_i (θ_i, Q_i) (the derivative of the area with respect to time) has to be zero. Because in both cases ($A_i = 0$ and $A_i = A_{\max i}$), the area is constant, for its derivative to be zero Q_i has to be also zero (control stops when all the area is invaded or the NIS is eradicated). In these cases, the equimarginal condition will be re-stated without the term corresponding to the marginal avoided costs and the marginal costs of Q_i.

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolecon.2010.02.001.

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