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):

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

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):

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

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:

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

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):

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

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):

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