



Spatially explicit control of invasive species using a reaction–diffusion model



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ABSTRACT

Invasive species, which can be responsible for severe economic and environmental damages, must often be managed over a wide area with limited resources, and the optimal allocation of effort in space and time can be challenging. If the spatial range of the invasive species is large, control actions might be applied only on some parcels of land, for example because of property type, accessibility, or limited human resources. Selecting the locations for control is critical and can significantly impact management efficiency. To help make decisions concerning the spatial allocation of control actions, we propose a simulation based approach, where the spatial distribution of the invader is approximated by a reaction–diffusion model. We extend the classic Fisher equation to incorporate the effect of control both in the diffusion and local growth of the invader. The modified reaction–diffusion model that we propose accounts for the effect of control, not only on the controlled locations, but on neighboring locations, which are based on the theoretical speed of the invasion front. Based on simulated examples, we show the superiority of our model compared to the state-of-the-art approach. We illustrate the use of this model for the management of Burmese pythons in the Everglades (Florida, USA). Thanks to the generality of the modified reaction–diffusion model, this framework is potentially suitable for a wide class of management problems and provides a tool for managers to predict the effects of different management strategies.

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1. Introduction

Invasive species (IS) are responsible for severe ecological damages and economic losses (Olson, 2006; Dehnen-Schmutz et al., 2007; Pysek and Richardson, 2010), and their management (e.g. control and/or eradication) is a challenging problem due to uncertainty about the species biological characteristics and limited resources with which to undertake control. Although the most cost-effective method for minimizing damage is one that prevents the arrival of non-indigenous species (Lodge et al., 2006; Keller et al., 2007), the implementation of such a strategy is not obvious when the potential invasiveness of a species is unknown and the species has commercial value (Keller and Springborn, 2013). As a consequence, the management of IS often starts long after their introduction, when ecological damages are visible and the species is already well established. In such a situation, the area occupied by the species can be large, and managers have to act with

limited resources in order to slow the invasion and/or eradicate the IS. Managers typically face the decision of where, when, how much and/or how often control has to be implemented. The optimal management of IS, reviewed in Epanchin-Niell and Hastings (2010), is discussed in a growing number of articles, in which biological models are coupled with efficient optimization routines (Mehta et al., 2007; Bogich et al., 2008; Hauser et al., 2009; Carrasco et al., 2010; Giljohann et al., 2011). But in many practical situations, the decision problem is spatially explicit by nature (Meier et al., 2014). Therefore, the problem is to decide where in the entire management area to allocate control effort. As the complexity of this optimization problem grows with the number of control units in the management area, finding the optimal management strategy among all possible alternatives becomes computationally intractable. Another important issue arises when there must be an accounting of the temporal dynamics of the invader population. Then, managers have to optimize their choices, not only for the current time step, but for possible scenarios in the future. One approach consists in using heuristic methods to find a sub-optimal management strategy (Schapaugh and Tyre, 2012; Nicol and Chadès, 2011). Although these methods should be favored first, heuristic methods can be hard to use in the most general case

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because of their computational complexity. And in some cases, even if the management area remains large, the areas where control can be implemented can be small. In this case, the challenge is not so much to compute the optimal control strategy, but to predict and compare the efficiency of the different options available to the manager. Then a natural approach is simulation based (Higgins et al., 2000; Grevstad, 2005; Provencher et al., 2007; Frid et al., 2013), which requires a dynamic, spatially explicit model of the invader population that takes into account the effects of control.

Reaction–diffusion (RD) models are general, spatially explicit models that use a partial differential equation to describe changes in population density over time and space. Although some limitations of these models are known (Svenning et al., 2014), they have been widely applied in ecology (Holmes et al., 1994; Cantrell and Cosner, 1996, 2003; Shigesada and Kawasaki, 1997; Bogich et al., 2008; Kaiser and Burnett, 2010; Acevedo et al., 2012; Leroux et al., 2013) and provide a good basis to describe the pattern of diffusion (Andow et al., 1990; Hastings et al., 2005). The basis of this model is described by Fisher’s equation with logistic growth (Fisher, 1937; Skellam, 1951):

$$\frac{\partial(n)}{\partial t} = D \underbrace{\left(\frac{\partial^2(n)}{\partial x^2} + \frac{\partial^2(n)}{\partial y^2} \right)}_{\text{Spread}} + \underbrace{\epsilon n \left(1 - \frac{n}{K} \right)}_{\text{Local growth}}, \quad (1)$$

where n is the species density at a given location (i.e. number of individuals per square kilometer), D is the diffusion coefficient (i.e. the rate at which individuals disperse), ϵ is the intrinsic rate of growth (i.e. the birth rate minus the death rate) and K is the so-called carrying capacity (i.e. the maximal density per location). The left term is responsible for the spread or diffusion of the species, and the right term for local population growth (here a logistic growth function). Classic RD models make the assumption that the invader is introduced at a given point in space and then diffuses in a homogeneous landscape in every direction with the same probability, such that movement can be characterized as a random walk. In an infinitely large and suitable landscape, the pattern of invasion is described by a growing circle centered on the point of first introduction. Although simple, this colonization pattern is quite general and can be used to model invasions in practice with reasonable computational complexity. But to be used to explore the control of IS, the Fisher equation (1) has to be modified in a way that accounts for the effect of control, not only on the local growth of the population, but on the diffusion process as well.

To account for the effect of control on population growth, a useful approach is based on the Schaefer model (Schaefer, 1957), extensively used in the field of fisheries economics. See for example (Clark, 1990) for a detailed analysis of the Schaefer model. This model is defined without any spatial component: if β is the control mortality (or fishing mortality or harvest rate) of the control method (or any removal method), the change in the population density is defined as follows: $\partial(n)/\partial t = \epsilon n(1 - n/K) - \beta n$. Several authors (Oruganti et al., 2002; Neubert, 2003; Kurata and Shi, 2008) extended this last equation for two dimensions by adding the diffusion term, as it appears in the original Fisher’s equation:

$$\frac{\partial(n)}{\partial t} = D \underbrace{\left(\frac{\partial^2(n)}{\partial x^2} + \frac{\partial^2(n)}{\partial y^2} \right)}_{\text{Spread}} + \underbrace{n \left(\epsilon \left(1 - \frac{n}{K} \right) - \beta \right)}_{\text{Local growth}}.$$

This modification is known as the Constant–Effort Harvesting model (CEH). For example, Neubert (2003) used this model to discuss the optimal locations of marine reserves, as well as the optimal level of harvesting. As one can see, the CEH model makes the assumption that the diffusion term is not affected by control (i.e. the spread term is unchanged), or equivalently that individuals cannot

be removed while dispersing. For invasive species this assumption is debatable, as far as they are generally controlled regularly over the year, thus both in-situ and during dispersal.

We propose to modify the diffusion term to explicitly account for the fact that individuals can be removed when they are diffusing. This results in a CEH model with an additional linear control mortality, where the density at any point is explicitly affected by the probability that immigrants have been removed.

We first compared the prediction of the CEH model and the modified RD model using a simulated data set. We then illustrated the use of this model for management of the Burmese python (*Python molurus bivittatus*) in the Everglades, Florida.

2. Materials and methods

2.1. Accounting for the effect of control actions

This section present the modified CEH model with a total linear removal rate. A complete proof of this new model is available in Appendix S1.

We assume that J control actions are available to the manager. The control actions are associated with the yearly control mortality $\alpha_{T_1}, \dots, \alpha_{T_J}$ and weights $r_{T_1}(\mathbf{x}), \dots, r_{T_J}(\mathbf{x})$. And let’s denote $C_{T_j} \subset \mathbb{R}^2$, $j = 1..J$, the spatial domain where control action T_j is applied. The different control actions can be for example, physical, chemical or biological. Then, the yearly control mortality is the added mortality created by the control action over a year (i.e. a reproduction cycle). Without loss of generality, we suppose that any point in space can be controlled by at most one control action, which implies that $\cap_{j=1}^J C_{T_j} = \emptyset$. In practice, a control action T_j can result from different control actions and the control mortality has to be computed accordingly. But in the model, T_j always appears as a single control action. As we consider the spatial problem of management, \mathbf{x} denotes a spatial coordinate: $\mathbf{x} = (x, y) \in \Omega \subseteq \mathbb{R}^2$, where Ω is the entire spatial domain or management area. Then $\mathbf{x} \in C_{T_j}$ means that location \mathbf{x} is controlled with control action T_j .

Formally, $r_{T_j}(\mathbf{x})$ is the probability that an immigrant to location \mathbf{x} crossed an area controlled by action T_j before arriving in \mathbf{x} . And thus, $\alpha_{T_j} \times r_{T_j}(\mathbf{x})$ is the probability that the individual will be removed before reaching location \mathbf{x} . In practice, obtaining an analytic value of $r_{T_j}(\mathbf{x})$ is not straightforward and an approximation is needed. We propose an intuitive way to compute $r_{T_j}(\mathbf{x})$ in the next section.

Finally, let $\beta(\mathbf{x})$ denote the yearly control mortality of the control action applied at location \mathbf{x} . If \mathbf{x} is not controlled, then $\beta(\mathbf{x}) = 0$ and if \mathbf{x} is controlled with action T_j , $\beta(\mathbf{x}) = \alpha_{T_j}$. In such a situation the population dynamic at location \mathbf{x} is described as follows:

$$\begin{aligned} \frac{\partial(n(\mathbf{x}, t))}{\partial t} = & D \left(\frac{\partial^2(n(\mathbf{x}, t))}{\partial x^2} + \frac{\partial^2(n(\mathbf{x}, t))}{\partial y^2} \right) - n(\mathbf{x}, t) \sum_{j=1}^J \alpha_{T_j} r_{T_j}(\mathbf{x}) \\ & + n(\mathbf{x}, t) \left(\epsilon \left(1 - \frac{n(\mathbf{x}, t)}{K} \right) - \beta(\mathbf{x}) \right) \end{aligned} \quad (2)$$

This modified RD model corresponds to the CEH model with an additional linear control mortality term and will be further denoted the LCM model. The only difference from the CEH model is the additional term $-n(\mathbf{x}, t) \sum_{j=1}^J \alpha_{T_j} r_{T_j}(\mathbf{x})$, which appears in the reaction term. As expected, not only the growth of the population is influenced by the control method at this location but also by control in its neighborhood, as control of dispersing individuals naturally decreases the number of individuals that are immigrating. One can

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