Mathematical Biosciences 215 (2008) 158–166

Contents lists available at ScienceDirect

Mathematical Biosciences

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

Biological invasions: Deriving the regions at risk from partial measurements

Michel Cristofol [a,b], Lionel Roques [c,*]

[a] LATP, CNRS/UMR 6632, CMI, Université de Provence, 39 rue Joliot Curie, 13453 Marseille Cedex 13, France
[b] Université d'Aix-Marseille III, IUT de St Jérôme, France
[c] INRA, UR546 Biostatistique et Processus Spatiaux, Domaine St Paul Site Agroparc, F-84914 Avignon, France

ARTICLE INFO

Article history:
Received 16 November 2007
Received in revised form 18 June 2008
Accepted 11 July 2008
Available online 24 July 2008

Keywords:
Reaction–diffusion
Biological invasions
Inverse problem
Habitat configuration
Carleman estimates
Simulated annealing

ABSTRACT

We consider the problem of forecasting the regions at higher risk for newly introduced invasive species. Favourable and unfavourable regions may indeed not be known a priori, especially for exotic species whose hosts in native range and newly-colonised areas can be different. Assuming that the species is modelled by a logistic-like reaction–diffusion equation, we prove that the spatial arrangement of the favourable and unfavourable regions can theoretically be determined using only partial measurements of the population density: (1) a local 'spatio-temporal' measurement, during a short time period and, (2) a 'spatial' measurement in the whole region susceptible to colonisation. We then present a stochastic algorithm which is proved analytically, and then on several numerical examples, to be effective in deriving these regions.

1. Introduction

Because of trade globalisation, a substantial increase in biological invasions has been observed over the last decades (e.g. Liebhold et al. [1]). These invasive species are, by definition [2], likely to cause economic or environmental harm or harm to human health. Thus, it is a major concern to forecast, at the beginning of an invasion, the areas which will be more or less infested by the species.

Because of their exotic nature, invading species generally face little competition or predation. They are therefore well adapted to modelling via single-species models.

Reaction–diffusion models have proved themselves to give good qualitative results regarding biological invasions (see the pioneering paper of Skellam [3], and the books [4,5] and [6] for review).

The most widely used single-species reaction–diffusion model, in homogeneous environments, is probably the Fisher–Kolmogorov [7,8] model:

$$u_t = D\Delta u + u(\mu - \gamma u), \quad t > 0, x \in \Omega \subset \mathbb{R}^N, \tag{1.1}$$

where $u = u(t,x)$ is the population density at time t and space position x, D is the diffusion coefficient, μ corresponds to the *constant* intrinsic growth rate, and $\frac{\mu}{\gamma}$ is the environment's carrying capacity. Thus γ measures the susceptibility to crowding effects.

On the other hand, the environment is generally far from being homogeneous. The spreading speed of the invasion, as well as the final equilibrium attained by the population are in fact often highly dependent on these heterogeneities [4,9–11]. A natural extension of (1.1) to heterogeneous environments has been introduced by Shigesada, Kawasaki, Teramoto [12]:

$$u_t = \nabla(D(x)\nabla u) + u(\mu(x) - \gamma(x)u), \quad t > 0, x \in \Omega \subset \mathbb{R}^N. \tag{1.2}$$

In this case, the diffusivity matrix $D(x)$, and the coefficients $\mu(x)$ and $\gamma(x)$ depend on the space variable x, and can therefore include some effects of environmental heterogeneity.

In this paper, we consider the simpler case where $D(x)$ is assumed to be constant and isotropic and γ is also assumed to be positive and constant:

$$u_t = D\Delta u + u(\mu(x) - \gamma u), \quad t > 0, x \in \Omega \subset \mathbb{R}^N. \tag{1.3}$$

The regions where μ is high correspond to favourable regions (high intrinsic growth rate and high environment carrying capacity), whereas the regions with low values of μ are less favourable, or even unfavourable when $\mu < 0$. In what follows, in order to obtain clearer biological interpretations of our results, we say that μ is a 'habitat configuration'.

With this type of model, many qualitative results have been established, especially regarding the influence of spatial heterogeneities of the environment on population persistence, and on the value of the equilibrium population density [4,9,13–15]. However, for a newly introduced species, like an invasive species at the beginning of its introduction, the regions where μ is high or low

---

* Corresponding author. Fax: +33 432722182.
E-mail addresses: michel.cristofol@univ-cezanne.fr (M. Cristofol), lionel.roques@avignon.inra.fr (L. Roques).

0025-5564/$ - see front matter © 2008 Elsevier Inc. All rights reserved.
doi:10.1016/j.mbs.2008.07.004

may not be known *a priori*, particularly when the environment is very different from that of the species native range.

In this paper, we propose a method of deriving the habitat configuration μ, basing ourselves only on partial measurements of the population density at the beginning of the invasion process. In Section 2, we begin by giving a precise mathematical formulation of our estimation problem. We then describe our main mathematical results, and we link them with ecological interpretations. These theoretical results form the basis of an algorithm that we propose, in Section 3, for recovering the habitat configuration μ. In Section 4, we provide numerical examples illustrating our results. These results are further discussed in Section 5.

2. Formulation of the problem and main results

2.1. Model and hypotheses

We assume that the population density u_γ is governed by the following parabolic equation:

$$\begin{cases} \partial_t u_\gamma = D\Delta u_\gamma + u_\gamma(\mu(x) - \gamma u_\gamma), & t > 0, x \in \Omega, \\ u_\gamma(t,x) = 0, \quad t > 0, x \in \partial\Omega, & (P_{\mu,\gamma}) \\ u_\gamma(0,x) = u_i(x) \text{ in } \Omega, & \end{cases}$$

where Ω is a bounded subdomain of $\mathbb{R}^d$ with boundary $\partial\Omega$. We will denote $Q := (0,+\infty) \times \Omega$ and $\Sigma := (0,+\infty) \times \partial\Omega$.

The growth rate function μ is *a priori* assumed to be bounded, and to take a known constant value outside a fixed compact subset Ω_1 of Ω:

$$\mu \in \mathscr{M} := \{\rho \in L^\infty(\Omega), -M \leqslant \rho \leqslant M \text{ a.e., and } \rho \equiv m \text{ in } \Omega \setminus \Omega_1\},$$

for some constants m, M, with $M > 0$; the notation ‘a.e.’ means ‘almost everywhere’, which is equivalent to ‘except on a set of zero measure’.

The initial population density $u_i(x)$ is assumed to be bounded (in $C^2(\overline{\Omega})$), and bounded from below by a fixed positive constant in a fixed closed ball $\mathscr{B}_\varepsilon \subset \Omega_1$, of small radius ε:

$$\mathscr{D} := \{\phi \geqslant 0, \phi \in C^2(\overline{\Omega}), \|\phi\|_{C^2(\Omega)} \leqslant \overline{u_i}, \phi \geqslant \underline{u_i} \text{ in } \mathscr{B}_\varepsilon, \}, \tag{2.4}$$

for some positive constants $\overline{u_i}$ and $\underline{u_i}$.

Absorbing (Dirichlet) boundary conditions are assumed.

Remark 2.1. Absorbing boundary conditions mean that the individuals crossing the boundary immediately die. Such conditions can be ecologically relevant in numerous situations. For instance for many plant species, seacoasts are lethal and thus constitute this kind of boundaries.

For technical reasons we have to introduce the subset Ω_1, such that, in the interface between Ω_1 and Ω, μ takes a known value m. This value is typically negative, indicating that, near the lethal boundary, the environment is unfavourable. This assumption is not very restrictive since, in fact, Ω_1 can be chosen as close as we want to Ω.

For precise definitions of the functional spaces L^2, L^∞ and C^2 as well as the other mathematical notations used throughout this paper, the reader can refer, e.g., to [16].

2.2. Main question

The main question that we presented at the end of Section 1 can now be stated: for any time-span (t_0, t_1), and any non-empty subset ω of Ω_1, is it possible to estimate the function $\mu(x)$ in Ω, basing ourselves only on measurements of $u_\gamma(t,x)$ over $(t_0, t_1) \times \omega$, and on a single measurement of $u_\gamma(t,x)$ in the whole domain Ω at a time $T' = \frac{t_0+t_1}{2}$?

2.3. Estimating the habitat configuration

Let $\tilde{\mu}$ be a function in $\mathscr{M}$, and let $\tilde{v}$ be the solution of the linear parabolic problem $(P_{\tilde{\mu},0})$. We define a functional G_μ, over $\mathbb{R}_+ \times \mathscr{M}$, by

$$G_\mu(\gamma, \tilde{\mu}) = \|\partial_t u_\gamma - \partial_t \tilde{v}\|^2_{L^2((t_0,t_1)\times\omega)} + \|\Delta u_\gamma(T',\cdot) - \Delta\tilde{v}(T',\cdot)\|^2_{L^2(\Omega)} + \|u_\gamma(T',\cdot) - \tilde{v}(T',\cdot)\|^2_{L^2(\Omega)},$$

where u_γ is the solution of $(P_{\mu,\gamma})$. This functional G_μ quantifies the gap between u_γ and $\tilde{v}$ on the set where u_γ has been measured.

Theorem 2.2. *The functions $\mu, \tilde{\mu} \in \mathscr{M}$ being given, we have:*

$$\|\mu - \tilde{\mu}\|^2_{L^2(\Omega_1)} \leqslant \frac{C}{\underline{u_i}^2} G_\mu(0, \tilde{\mu}),$$

for all $\tilde{\mu} \in \mathscr{M}$ and for some positive constant $C = C(\Omega, \Omega_1, \omega, \mathscr{B}_\varepsilon, D, t_0, t_1, \underline{u_i}/\overline{u_i})$.

The proof of this result is given in Appendix A.1. It bears on a Carleman-type estimate.

Biological interpretation: This stability result means that, in the linear case corresponding to Malthusian populations ($\gamma = 0$), two different habitat configurations $\mu, \tilde{\mu}$ cannot lead to close population densities $u_0, \tilde{v}$. Indeed, having population densities that are close to each other in the two situations, even on a very small region ω, during a small time period (t_0, t_1), and in the whole space Ω at a single time $T\prime$, would lead to small G_μ values, and therefore, from Theorem 2.2, to close values of the growth rate coefficients μ and $\tilde{\mu}$.

Theorem 2.2 implies the following uniqueness result:

Corollary 2.3. *If v is a solution of both $(P_{\mu,0})$ and $(P_{\tilde{\mu},0})$, then $\mu = \tilde{\mu}$ a.e. in Ω_1, and therefore in Ω.*

Biological interpretation: In the linear case ($\gamma = 0$), if two habitat configurations $\mu, \tilde{\mu}$ lead to identical population densities $u_0, \tilde{v}$, even on a very small region ω, during a small time period (t_0, t_1), and in the whole space Ω at a single time $T\prime$, then these habitat configurations are identical.

Next we have the following result:

Theorem 2.4. *We have*[1] $|G_\mu(0, \tilde{\mu}) - G_\mu(\gamma, \tilde{\mu})| = \mathscr{O}(\overline{u_i}^3)$, as $\overline{u_i} \to 0$.

The proof of this result is given in Appendix A.2.

Biological interpretation: Assume that the habitat configuration μ is not known, but that we have measurements of the population density u_γ, governed by the full non-linear model (1.3). Consider a configuration $\tilde{\mu}$ in $\mathscr{M}$ such that the population density $\tilde{v}$ obtained as a solution of the linear model $(P_{0,\tilde{\mu}})$ has values close to those taken by the population density u_γ, in the sense that $G_\mu(\gamma, \tilde{\mu})$ is close to 0. If the initial population density is far from the environment carrying capacity, then $\overline{u_i} \ll \frac{\mu}{\gamma}$, $\overline{u_i}$ is small and, from Theorem 2.4, $G_\mu(0, \tilde{\mu})$ is also close to 0. Thus Theorem 2.2 implies that the habitat configuration $\tilde{\mu}$ is an accurate estimate of μ. In Section 3, we propose an algorithm to obtain explicitly such estimates of μ.

Remark 2.5. In fact, the term $\mathscr{O}(\overline{u_i}^3)$ increases exponentially with time t_1. Thus, obtaining accurate estimates of μ require, in practice, to work with small times i.e. at the beginning of the invasion.

2.4. Forecasting the fate of the invading population

The knowledge of an L^2-estimate $\tilde{\mu}$ of μ enables us to give an estimate of the asymptotic behaviour of the solution u_γ of $(P_{\mu,\gamma})$, as $t \to +\infty$, and especially to know whether the population will

---

[1] Two functions $f(\mu, \tilde{\mu}, u_i, \underline{u_i}, \overline{u_i}, \gamma)$ and $g(\mu, \tilde{\mu}, u_i, \underline{u_i}, \overline{u_i}, \gamma)$, are written $f = \mathscr{O}(g)$ as $g \to 0$ if there exists a constant $K > 0$, independent of μ, $\tilde{\mu}$, u_i, $\underline{u_i}$, $\overline{u_i}$ and γ, such that $| f | \leqslant K | g |$ for g small enough.