

Structured population model with diffusion in structure space

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Abstract A structured population model is described and analyzed, in which individual dynamics may be stochastic. The model consists of a PDE of advection-diffusion type in the structure variable. The population may represent, for example, the density of infected individuals structured by pathogen density x , $x \geq 0$. The individuals with density $x = 0$ are not infected, but rather susceptible or recovered. Their dynamics is described by an ODE with a source term that is the exact flux from the diffusion and advection as $x \rightarrow 0^+$. Infection/reinfection is then modeled by distributing some fraction of these individuals into the infected class, but distributed in the structure variable through a probability density function. Existence of a global-in-time solu-

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tion is proven, as well as a classical bifurcation result about equilibrium solutions: a net reproduction number R_0 is defined that separates the case of only the trivial equilibrium existing when $R_0 < 1$ from the existence of another —nontrivial— equilibrium when $R_0 > 1$. Numerical simulation results are provided to show the stabilization towards the positive equilibrium when $R_0 > 1$ and towards the trivial one when $R_0 < 1$, result that is not proven analytically. Simulations are also provided to show the Allee effect that helps boost population sizes at low densities.

1 Introduction

Modeling the dynamics of structured populations (where the structure may be age, size or other physiological indicator) has been an active research area, at least since the book edited by Metz, J.A.J. and Diekmann (1986) sparked both relevant biological applications (de Roos and Persson, 2013) and interesting mathematical problems (Diekmann et al, 1998; Thieme, 1988). In this type of model, one distinguishes between the internal dynamics (i.e. how the structure evolves in an individual) and the overall population dynamics of the number of individuals and of the distribution of the structure in them.

Beyond population dynamics and ecology, this methodology has been applied to immuno-epidemiological models where the infected population is structured through their pathogen load and immune level (Angulo et al, 2013a,b; Gandolfi et al, 2015; Gilchrist and Sasaki, 2002), and to metapopulation models in which individuals correspond to patches, and the structure represents the population size in the patch (Gyllenberg and Hanski, 1992; Gyllenberg and Metz, 2001).

Generally, the internal dynamics has been assumed to be described by a system of ordinary differential equations, leading at the population level to a partial differential equation of transport type (Perthame, 2007), though different mathematical approaches have been used Diekmann et al (1998, 2007).

Hadeler (2010) extended the method to the case in which the underlying individual dynamics includes a stochastic component. Hence, the overall population density is described through a partial differential equation including diffusion in the structure variables, for which appropriate boundary conditions were sought. This approach was followed in recent years by Farkas and Hinow (2011) and Calsina and Farkas (2012) through the introduction of Wentzell boundary conditions.

Restricting ourselves to the case where the structure variable, x , is one-dimensional and non-negative, we show here how the standard theory of degenerate diffusion (as first proposed by Feller 1951; 1952; 1954) leads to a simple and rather complete analysis.

Although a multi-dimensional internal state may be more realistic in many interesting applications, there are also cases where the assumption of a one-dimensional non-negative structure variable is relevant. We refer mainly to two applications mentioned above. The first one is epidemiological: the individuals being modeled are infectives (infected/infectious), and x describes their pathogen load. Alternatively, we consider a metapopulation model: individuals represent patches, and x describes the population size in that patch.

An interesting feature of both cases is that individuals at $x = 0$ are qualitatively different from the others: in the first case corresponding to susceptible (not infected)

individuals and in the second case to empty patches. In what follows we will use interchangeably the terms colonization/infection referring to the case when an individual moves from 0 to a positive x -state, and extinction/recovery referring to the case where an individual moves from a positive x -state to 0.

Models based on transport equations in the x -space have serious problems dealing with the special state at $x = 0$; for instance in many structured metapopulation models (Gyllenberg and Hanski, 1992; Gyllenberg and Metz, 2001) there are no empty patches, since, even if they are created by catastrophes that completely wipe out a local population, they get immediately recolonized by a continuous flow of immigrants.

We show in this article how stochastic dynamics at the individual level naturally solves the problem without any special assumption. In the next Section we shall present the model, introducing also some properties of one-dimensional diffusion for which we mainly refer to (Karlin and Taylor, 1981). In Section 3, after stating some properties of the semigroup associated to one-dimensional parabolic equations (Feller, 1952), we set the problem in abstract form and prove global existence of solutions (several technical details are relegated to the Appendix). In Section 4, we find conditions for instability of the trivial equilibrium and observe that they correspond to those for existence of a unique positive equilibrium that is explicitly specified. Section ?? shows some numerical results that illustrate the properties of the solutions, while comments and possible extensions are left to the Discussion Section.

2 The model

{sec:model}

2.1 Feller diffusion with logistic growth

We shall assume that the dynamics of pathogen load within each individual (or population in each patch) follows a diffusion process

{base_SDE}

$$dX_t = r(X_t)dt + \sqrt{2a(X_t)}dw_t \quad x > 0, t > 0, \quad (1)$$

where $r(x)$ represents the infinitesimal drift and $2a(x)$ the infinitesimal variance. In what follows, we shall generally assume

$$r(x) = \bar{r}x(1 - cx), \quad a(x) = \bar{a}x, \quad (2) \quad \{\text{logistic}\}$$

a process that has been studied in several recent papers (Cattiaux et al, 2009; Lambert, 2005) and is usually referred as “Feller diffusion with logistic growth” (Feller, 1951). All constants are assumed to be strictly positive; moreover, without loss of generality we set $\bar{a} = 1$, since this just amounts to rescaling the x -axis. Finally, note that $K = 1/c$ can be considered the carrying capacity, to which the system would tend in the absence of stochasticity.

With this choice of r and a , absorption into $x = 0$ is certain (Cattiaux et al, 2009; Karlin and Taylor, 1981). In the terminology of Feller (Feller, 1954), $x = 0$ is an exit boundary while $x = +\infty$ is a natural boundary. This means that recovery from infection [local extinction] is certain, although the time required may be extremely long.

Assuming that the process X_t is absorbed at 0 once it reaches it (Feller, 1954, other choices are possible; see), one can define the transition function $p_0(t, x; \xi)$ with the

property that, for each Borel set $B \subset (0, \infty)$,

$$\mathbb{P}(X_t \in B | X_0 = \xi) = \int_B p_0(t, x; \xi) dx. \quad (3) \quad \{\text{p0}\}$$

Because of absorption at 0, $p_0(t, \cdot; \xi)$ is a defective density, i.e.

$$\int_0^\infty p_0(t, x; \xi) dx < 1.$$

A useful quantity of the process is its scale function (Karlin and Taylor, 1981)

$$\{\text{scale}\} \quad S(x) = \int_{x_0}^x \exp\left\{-\int_{x_0}^z \frac{r(\xi)}{a(\xi)} d\xi\right\} dz = \int_{x_0}^x e^{-\bar{r}(\zeta - x_0) + \bar{r}c(\zeta^2 - x_0^2)/2} d\zeta, \quad (4)$$

where the rightmost expression is obtained using (2) and $\bar{a} = 1$.

Through it, one obtains the following result for the probability of reaching a certain level x starting from ξ (see, for instance, (Karlin and Taylor, 1981), keeping in mind that absorption at 0 is certain for X_t).

Proposition 1 *Let $0 < \xi < x$. Then,*

$$\{\text{prob_touch_x}\} \quad \mathbb{P}(X_t \text{ ever reaches } x | X_0 = \xi) = \frac{S(\xi) - S(0)}{S(x) - S(0)}, \quad (5)$$

where S is the scale function (4).

It is clear that the choice of x_0 in (4) is irrelevant for the computation of (5); it is also clear that we can multiply S by any constant without changing (5) and, therefore, we shall compute it as

$$\{\text{p_reach_x}\} \quad \mathbb{P}(X_t \text{ ever reaches } x | X_0 = \xi) = \frac{\int_0^\xi e^{\bar{r}(\zeta - K)^2/(2K)} d\zeta}{\int_0^x e^{\bar{r}(\zeta - K)^2/(2K)} d\zeta} \quad (6)$$

where $K = 1/c$.

It is clear that most arguments would remain the same with different choices of the functions a and r as long as $x = 0$ is an exit boundary, and $x = +\infty$ is a natural boundary. This fact will be exploited in the numerical examples, where $r(\cdot)$ is modified to allow for an Allee effect.

2.2 The equation at the population level

The Kolomogorov forward equation associated to the process X_t with absorbtion at $x = 0$ is

$$u_t(t, x) = \partial_x [(a(x)u(t, x))_x - r(x)u(t, x)], \quad x, t > 0,$$

with no boundary conditions (Feller, 1954).

Feller (1954) also introduced the *elementary return process* in which particles absorbed at 0 jump (after an exponential waiting time) to some state $x > 0$. Assuming, for the sake of simplicity, that the distribution of the jumps has a density $q(x)$, the elementary return process has a density $u(t, x)$ on the positive axis that is the (weak) solution of

$$u_t(t, x) = \partial_x [(a(x)u(t, x))_x - r(x)u(t, x)] + \lambda E(t)q(x), \quad t, x > 0, \quad (7) \quad \{\text{forw_elem}\}$$

where $E(t)$ represents the probability that the process is at 0, and $1/\lambda$ is the mean waiting time at 0; $E(\cdot)$ satisfies the equation

$$E'(t) = -\lambda E(t) + \lim_{x \rightarrow 0^+} \left[(a(x)u(t, x))_x - r(x)u(t, x) \right]. \quad (8) \quad \{\text{ODE_E}\}$$

We assume now that the population consists of an infinite number of individuals whose infection level, if infected, is described by equation (1). Furthermore, infected individuals produce (at a rate $\beta(x)$) propagules that may infect susceptible (i.e.

infection-free) individuals. Alternatively, we assume an infinite number of patches characterized by their population size x ; propagules produced by each patch may colonize empty patches.

Because of the infinite number of patches, one can equate probabilities with densities (the argument can be made rigorous employing, for example, the methods of ?). Then, the function $u(t, x)$, representing the density at time t of individuals in a given state $x > 0$ (i.e. $\int_{x_1}^{x_2} u(t, x) dx$ is the fraction of individuals with infection load between x_1 and x_2 at time t , or the fraction of patches whose population size is between x_1 and x_2) and $E(t)$, representing the fraction of infection-free individuals (empty patches), will satisfy equations (7) and (8), with the caveat that λ will not be a constant, but will rather depend on current infection load.

More specifically, we shall assume $\lambda(t) = \int_0^\infty \beta(x)u(t, x) dx$, where the function β (the rate at which infectives at state x produce infectious propagules) includes the probability of reaching a susceptible.

In summary, for $t > 0$, we shall consider the system

$$\{\text{linear_system}\} \quad \left\{ \begin{array}{l} E'(t) = -\lambda(t)E(t) + \lim_{x \rightarrow 0^+} \left[(a(x)u(t, x))_x - r(x)u(t, x) \right], \\ u_t(t, x) = \partial_x [(a(x)u(t, x))_x - r(x)u(t, x)] + \lambda(t)E(t)q(x), \quad x > 0, \\ \lambda(t) = \int_0^\infty \beta(x)u(t, x) dx, \end{array} \right. \quad (9)$$

where the dynamics of the susceptibles (respectively, empty patches) E is modeled with a classical sink represented as the product of the force of infection λ and the susceptible population size (respectively, unit colonization rate times the density of empty patches), and a source representing the rate at which infected individuals re-

cover (respectively, the rate at which colonized patches die out), $\lim_{x \rightarrow 0^+} [(a(x)u(t, x))_x - r(x)u(t, x)]$ —the flux towards 0 of the second equation of (9).

3 Abstract formulation

{sec:abstract}

3.1 Semigroup associated to 1-dimensional parabolic equations

In a series of papers Feller proved some fundamental results about 1-dimensional parabolic equations, and their relationship with diffusion processes. In particular what concerns us is the following result.

Theorem 2 (Theorem 15.2 of (Feller, 1952)) *Let $a(\cdot) > 0$ and $r(\cdot)$ be continuous functions on the (possibly infinite) interval (r_1, r_2) . Let Ω^* be the operator*

$$(\Omega^*g)(x) = \frac{d}{dx} \left[\frac{d}{dx} (a(x)g(x)) - r(x)g(x) \right], \quad (10) \quad \{\text{omega*}\}$$

*defined on the set of functions g smooth enough on (r_1, r_2) that $\Omega^*g \in L^1(r_1, r_2)$.*

If none of the boundaries are regular, then Ω^ is the generator of a strongly continuous positive semigroup T_t^* in $L^1(r_1, r_2)$.*

Furthermore, if at least one boundary is of exit type, then T_t^ is strictly norm-decreasing.*

This semigroup represents the evolution of the measure associated to the diffusion process (1). More precisely, if g represents the distribution of X_0 , i.e. $\mathbb{P}(X_0 \in A) = \int_A g(x) dx$ for each Borel set A , then

$$\int_B (T_t^*g)(x) dx = \mathbb{P}(X_t \in B) \text{ for each Borel set } B \subset (0, \infty).$$

Using the transition density (3), one can write

$$(T_t^*g)(\cdot) = \int_0^\infty p_0(t, \cdot; \xi) g(\xi) d\xi.$$

T_t^* is the (restriction of the) adjoint of the semigroup T_t on $C_0(0, \infty)$, where

$$(T_t f)(x) = \mathbb{E}(f(X_t) | X_0 = x),$$

whose generator is Ω defined by

$$\Omega f = af'' + rf'. \quad (11)$$

Note that T_t^* can be extended to the space of Borel measures (and, actually, is naturally defined there).

3.2 The semigroup on weighted L^1 -spaces

We wish to prove that, under our assumptions on a and r , T_t^* is also a strongly continuous semigroup on the space $L_w^1(0, \infty)$ that we define as the weighted $L^1(0, \infty)$ -space with weight $w(x) = 1 + x^2$. This is necessary since we will allow in (9) for unbounded functions $\beta(x)$ that satisfy $\beta(x) \leq M(1 + x^2)$.

For this purpose we need the following two simple Lemmas.

{lemma1}

Lemma 1 *Let $b > 0$. Then*

$$\lim_{L \rightarrow \infty} \sup_{0 < \xi \leq L-b} \int_L^\infty x^2 p_0(t, x; \xi) dx = 0. \quad (12)$$

{lemma2}

Lemma 2 *Let $b > 0$, $K = 1/c$ and let $L > K$ be such that $\int_K^L e^{\bar{r}c \frac{x^2}{2}} dx > 1$. Then, there exists $C > 0$ such that*

$$\sup_{\xi \geq L-b} \frac{\int_L^\infty x^2 p_0(t, x; \xi) dx}{\xi^2} \leq C. \quad (13)$$

Note that these two Lemmas implicitly show that, for each $\xi > 0$ and $t > 0$, $p_0(t, \cdot; \xi) \in L_w^1(0, \infty)$. It is easy to see from this that, if $g \in L_w^1(0, \infty)$, then $T_t^* g$ also belongs to $L_w^1(0, \infty)$ for $t \geq 0$.

Based on these results we can prove the strong continuity of the semigroup operator on the weighted L^1 -space.

{prop:C0w}

Proposition 3 T_t^* restricted to $L_w^1(0, \infty)$ is strongly continuous.

Again the proof is left to the Appendix. Looking at the arguments used, it is quite clear that a similar proof can be carried out for any weight $w(x) = 1 + x^p$ with $p > 0$, but the context considered here led us to look only at $p = 2$.

3.3 Semilinear problem

Note that problem (9) can be written in abstract form as

$$\begin{cases} u'(t) = \Omega^* u(t) + F(u(t)), \\ u(0) = u_0, \end{cases} \quad (14) \quad \{\text{abstract}\}$$

where $F : L_w^1(0, \infty) \rightarrow L_w^1(0, \infty)$ is

$$[F(u)](x) = \left(\int_0^\infty \beta(\xi) u(\xi) d\xi \right) \left(1 - \int_0^\infty u(\xi) d\xi \right) q(x). \quad (15) \quad \{F(u)\}$$

We then have

{prop1}

Proposition 4 Assume that $\beta(x) \leq M(1 + x^2)$ (in some examples we shall use $\beta(x) = \beta_1 x + \beta_2 x^2$) and q a density function with bounded support.

Then for each $u_0 \in L_w^1$ there exists a unique (mild) solution of (14) on some interval $[0, T]$.

The result follows easily from standard results [?](#), since under the assumptions F is a Lipschitz operator on $L_w^1(0, \infty)$.

Note that in the formulation (14) we avoid considering the dynamics of the boundary accumulation function E explicitly but rather we just define it as $E(t) = 1 - \int_0^\infty u(t, x) dx$. For the solution to make sense from the biological point of view, we then need to prove that, starting from $u_0 \geq 0$ with $\|u_0\|_1 \leq 1$, it follows that the solution u of (14) satisfies $u(t) \geq 0$ and $\|u(t)\|_1 \leq 1$ for all $t > 0$. Proving this, as well as the boundedness of $\|u(t)\|_{1,w}$, will also ensure that the solution is global. Thus, we prove the following:

{mainthm}

Proposition 5 *Let $u_0 \geq 0$ with $\|u_0\|_1 \leq 1$ and let u be the solution of (14) on $[0, T]$. Then, $u(t) \geq 0$ and $\|u(t)\|_1 \leq 1$ for all $t \in [0, T]$.*

The details of the proof are left to the Appendix. It provides a probabilistic construction of $E(t) = 1 - \int_0^\infty u(t, x) dx$ and $u(t, x)$. Precisely $E(t)$ is obtained as the series $\sum_{i=0}^\infty E_i(t)$ where

$$E_0(t) = E_0 \exp \left\{ - \int_0^t \lambda(v) dv \right\}$$

is the the fraction of individuals that have never been infected in the interval $[0, t]$. $E_1(t)$ are the individuals infection-free at t that were infected in a single interval in $[0, t)$, $E_i(t)$ those that have been infected in i separate intervals within $[0, t)$. The density $u(t, x)$ is written as an analogous series of corresponding terms.

In order to ensure global existence we would also need to prove boundedness of the solution in weighted norm. Assuming that q has bounded support, this follows easily from Lemma 1.

4 Equilibria and stability

{sec:equil}

Equation (14) clearly has the trivial equilibrium $u \equiv 0$ (corresponding to $E = 1$).

Concerning its stability, we shall prove the following threshold property.

Theorem 6 *The trivial equilibrium is asymptotically stable (respectively, unstable)*

for (14) if $R_0 < 1$ (respectively, $R_0 > 1$), where

$$\begin{aligned} R_0 &= \int_0^\infty \mathbb{E} \left(\int_0^{\tau_x} \beta(X_s) ds | X_0 = x \right) q(x) dx \\ &= \int_0^\infty \int_0^x \int_t^\infty e^{\frac{\bar{r}}{K}(t-\xi)(\frac{t+\xi}{2}-K)} \frac{\beta(\xi)}{\xi} d\xi dt q(x) dx. \end{aligned} \quad (16) \quad \{R_0\}$$

The definition of R_0 on the first line of (16) corresponds to the usual interpretation of the net reproduction number: R_0 represents the expected number of propagules produced by an initial colonizing group (starting with size x according to the distribution q) before the patch becomes extinct (τ_x represents the absorption time, conditional on initial size x). If each new group of colonizers produces on average more than one successful propagule (assuming that all patches are available), then the metapopulation will persist, even though each population will eventually become extinct; otherwise it will not.

The expression on the second line of (16) (valid under (2) and $\bar{a} = 1$) comes from standard theory of diffusion processes (Karlin and Taylor, 1981) and yields an explicit method to compute R_0 . Note that the nature of the problem implies that $\beta(0)$ so that, if $\beta(\cdot)$ is Lipschitz,

Proof The equilibrium $u \equiv 0$ is asymptotically stable (respectively, unstable) for (14) if the growth bound of the semigroup generated by $\Omega^* + F'(0)$ is negative (respec-

tively, positive), where $F'(0)$ is the operator on L_w^1 defined by

$$[F'(0)u](x) = q(x) \int_0^\infty \beta(\xi) u(\xi) d\xi.$$

As the semigroup T_t^* generated by Ω^* is positive (Engel and Nagel, 2000) and $F'(0)$ is compact (it has one-dimensional range), the growth bound corresponds to the spectral bound

$$\{s_{\text{star}}\} \quad s(\Omega^* + F'(0)) = \max \{ \Re \lambda : \lambda \in \sigma(\Omega^* + F'(0)) \}. \quad (17)$$

As both $F'(0)$ and T_t are positive, T_t has negative growth bound, and $F'(0)$ is compact, it is well known (Engel and Nagel, 2000) that

$$\begin{aligned} s(\Omega^* + F'(0)) &< 0 \text{ (respectively, } > 0) \\ \iff \rho((-\Omega^*)^{-1}F'(0)) &< 1 \text{ (respectively, } > 1). \end{aligned}$$

In order to have a criterion that is easier to interpret and evaluate, we prefer to see $(-\Omega^*)^{-1}F'(0)$ as the (restriction of the) adjoint of $K(-\Omega)^{-1}$, an operator in the space

$$C_w(0, \infty) = \{f \in C[0, \infty) : f(0) = 0, |f(x)|/(1+x^2) \text{ is bounded}\}$$

endowed with the norm $\|f\|_w = \sup_{x \in (0, \infty)} \{|f(x)|/(1+x^2)\}$, with K defined in $C_0(0, +\infty)$ as

$$\{K(\mathfrak{f})\} \quad [K(f)](x) = \beta(x) \int_0^\infty q(\xi) f(\xi) d\xi. \quad (18)$$

Remember that we have assumed q has compact support, so the integral makes sense.

Further, because of the assumptions on β K maps into $C_w(0, \infty)$.

It is clear that the adjoint of $K(-\Omega)^{-1}$ (which is defined in an appropriate space of measures on $(0, \infty)$) coincides with $(-\Omega^*)^{-1}F'(0)$ when restricted to $L_w^1(0, \infty)$.

Moreover, as $K(-\Omega)^{-1}$ has one-dimensional range, the same is true for its adjoint, whose range then coincides with that of $(-\Omega^*)^{-1}F'(0)$. It then follows that

$$R_0 = \rho(K(-\Omega)^{-1}) = \rho((-\Omega^*)^{-1}F'(0))$$

and, by the above equivalence between negative (respectively, positive) spectral bound and spectral radius smaller (respectively, larger) than 1, it follows that the trivial equilibrium is asymptotically stable if $R_0 < 1$, and unstable if $R_0 > 1$. It only remains to be seen that R_0 here defined coincides with (16).

Let h be an eigenvector of $K(-\Omega)^{-1}$ with eigenvalue σ . Since the range of K is the space generated by β , necessarily $h = \beta$ and $\sigma = R_0$; hence

$$K(-\Omega)^{-1}\beta = R_0\beta.$$

Let $f = (-\Omega)^{-1}\beta$ so that $\Omega f = -\beta$. From $Kf = R_0\beta$, we obtain, using the definition (18),

$$R_0 = \int_0^\infty q(x)f(x)dx. \quad (19) \quad \{\text{RO}_f\}$$

The equation $\Omega f = -\beta$ is

$$a(x)f''(x) + r(x)f'(x) = -\beta(x), \quad x \in (0, \infty) \quad (20) \quad \{\Omega_{\text{h}}\}$$

and its solution can be written, using the Green function

$$G(x, \xi) = \frac{1}{\xi} \int_0^{\min\{x, \xi\}} e^{(r/2K)[(t-K)^2 - (\xi-K)^2]} dt, \quad 0 < x, \xi, \quad (21) \quad \{\text{Green}\}$$

as

$$\begin{aligned}
f(x) &= \int_0^\infty G(x, \xi) \beta(\xi) d\xi \\
&= \int_0^x \int_0^\xi e^{(r/2K)[(t-K)^2 - (\xi-K)^2]} dt \frac{\beta(\xi)}{\xi} d\xi \\
&\quad + \int_x^\infty \int_0^x e^{(r/2K)[(t-K)^2 - (\xi-K)^2]} dt \frac{\beta(\xi)}{\xi} d\xi \\
&= \int_0^x \int_t^\infty e^{(r/2K)[(t-K)^2 - (\xi-K)^2]} \frac{\beta(\xi)}{\xi} d\xi dt.
\end{aligned} \tag{22} \quad \{\mathbf{h}(\mathbf{x})\}$$

It is immediate to see that (22) is indeed solution of (20) when $a(x) = x$ and $r(x) = \bar{r}x(1 - x/K)$ and yields the expression in the second line of R_0 .

As for its interpretation, note that, defining for $0 < a < x < b$,

$$\tau_x^{a,b} = \inf\{t : X_t = a \text{ or } X_t = b \mid X_0 = x\},$$

$f_{a,b}(x) = \mathbb{E} \left(\int_0^{\tau_x^{a,b}} \beta(X_s) ds \mid X_0 = x \right)$ satisfies (Karlin and Taylor, 1981, 15.3.3) equation (20) in (a, b) with $f_{a,b}(a) = f_{a,b}(b) = 0$. Moreover, $f_{a,b}(x)$ has an explicit expression (Karlin and Taylor, 1981, 15.3.11) whose limit for $b \rightarrow \infty$ and $a \rightarrow 0^+$ is (22).

On the other hand, since

$$\mathbb{P}(X_{\tau_x^{a,b}} = b \mid X_0 = x) \rightarrow 0 \text{ as } b \rightarrow \infty \text{ and } a \rightarrow 0^+,$$

it follows that

$$\lim_{\substack{a \rightarrow 0^+ \\ b \rightarrow \infty}} \mathbb{E} \left(\int_0^{\tau_x^{a,b}} \beta(X_s) ds \mid X_0 = x \right) = \mathbb{E} \left(\int_0^{\tau_x} \beta(X_s) ds \mid X_0 = x \right).$$

Hence, the expression on the first line of (16) is equal to that on second line.

Next we consider positive equilibria. At an equilibrium \bar{u} , necessarily

$$\lambda = \int_0^\infty \beta(x) \bar{u}(x) dx$$

is a constant. Then $(\bar{E}, \bar{u}(x))$ will be the stationary distribution of the elementary return process with holding time rate λ . Using the explicit form provided by (Peng and Li, 2013), we obtain

$$\bar{u}(y) = \frac{\int_0^\infty q(x) G(x, y) dx}{\frac{1}{\lambda} + \int_0^\infty q(x) \int_0^\infty G(x, y) dy dx}. \quad (23) \quad \{\bar{u}\}$$

Let us define

$$\Psi = \int_0^\infty q(x) \int_0^\infty G(x, y) dy dx = \int_0^\infty q(x) \mathbb{E}(\tau_x) dx.$$

Then, substituting (23) in the definition of λ , we obtain

$$\lambda = \frac{\int_0^\infty \beta(y) \int_0^\infty q(x) G(x, y) dx dy}{\frac{1}{\lambda} + \Psi},$$

and, noting that the numerator is exactly R_0 , we have

$$\lambda = \frac{R_0 - 1}{\Psi}. \quad (24) \quad \{\lambda_{eq}\}$$

Of course, this corresponds to a positive solution if, and only if, $R_0 > 1$. We have thus obtained the following result.

Theorem 7 *Problem (14) has a positive equilibrium if and only if $R_0 > 1$. It can be written explicitly as*

$$\begin{aligned} \bar{u}(y) &= \frac{R_0 - 1}{R_0 \Psi} \int_0^\infty q(x) G(x, y) dx \\ &= \frac{R_0 - 1}{R_0 \Psi y} \int_0^y e^{(\bar{r}/2K)[(t-K)^2 - (y-K)^2]} \int_t^\infty q(x) dx dt. \end{aligned} \quad (25) \quad \{\text{eq_pos}\}$$

Correspondingly,

$$\bar{E} = 1 - \int_0^\infty \bar{u}(y) dy = 1/R_0.$$

It is not difficult to check that (25) is indeed a solution of (14).

The characteristic equation at \bar{u} can be used in order to analyze local stability of the positive equilibrium, but we shall not perform such analysis here.

5 Numerical results

We approximate the solution of (9) using finite differences in explicit form, that is backward in time with the x -derivatives discretized at the previous time level. Specifically, we let $\Delta x > 0$ and $\Delta t > 0$ be the discretization parameters (that will have to satisfy a stability condition) and we let the final time of simulation T be an integer multiple of Δt and $N = \frac{T}{\Delta t} \in \mathbb{N}$. Similarly, we let $\max \text{supp}(u_0)$ and $\max \text{supp}(q)$ be integer multiples of Δx , and define $N_{q_0} = \frac{\sup\{\text{supp}(q)\}}{\Delta x}$ and $N_{u_0} = \frac{\sup\{\text{supp}(u_0)\}}{\Delta x}$. We choose next an integer $M > \max\{N_{q_0}, N_{u_0}\}$ large enough that the practical computational support of u in x for the time span $[0, T]$ will not exceed $M\Delta x$. We introduce the computational time-grid

$$t^n = n\Delta t, \quad 0 \leq n \leq N,$$

and the computational x -grid

$$x_j = j\Delta x, \quad 0 \leq j \leq M.$$

For a function f of the structure variable x we shall use the notation $f_j = f(x_j)$ and for a function g of time t we shall use the notation $g^n = g(t^n)$. We want to find approximations U_j^n of $u(t^n, x_j)$ for $0 \leq n \leq N$ and $1 \leq j \leq M$. The support in x of the approximations grow by Δx at each time-step Δt . However, the magnitude of most

of the approximate values on the right tail are so small that we can actually neglect them without introducing virtually any errors. The numerical algorithm is

$$\left\{ \begin{array}{l} U_0^n - U_{M+1}^n = 0, \quad 0 \leq n \leq N, \\ I^n = \sum_{j=1}^M U_j^n, \quad \Lambda^n = \sum_{j=1}^M \beta_j U_j^n, \quad E^n = 1 - I^n, \quad 0 \leq n \leq N, \\ \frac{U_j^{n+1} - U_j^n}{\Delta t} = \frac{a_{j+1}U_{j+1}^n - 2a_jU_j^n + a_{j-1}U_{j-1}^n}{(\Delta x)^2} - \frac{r_{j+1}U_{j+1}^n - r_{j-1}U_{j-1}^n}{2\Delta x} \\ \quad + \Lambda^n E^n q_j, \quad 1 \leq j \leq M, \quad 0 \leq n \leq N-1. \end{array} \right. \quad (26)$$

For our simulations we use for both u_0 and q truncated inverted parabolas with support between their zeros at $x = 0$ and $x = 0.0333$, and at $x = 0$ and $x = 0.6667$, respectively. Since q must be a probability density function, we multiply the quadratic $x(0.6667 - x)$ by the factor that makes its integral exactly equal to 1. For normalization purposes we take $\bar{a} = c = 1$, and to ensure stability we need $\Delta t < \frac{\Delta x}{2aM}$, where we use $M = \frac{3}{\Delta x}$ to establish the computational x -support of the solution u to be $[0, \frac{3}{c}]$. We actually use another parameter in the simulations, $\eta \geq 0$, to slightly modify the function r in the flux term to allow for an Allee effect: $r(x) = \bar{r}(x - \eta)(1 - cx)$.

Next we present the solution corresponding to $\alpha = 4.8$, $\kappa = 0.3333$, $\bar{r} = 9$, $\eta = 0$, $T = 50$, $\Delta x = 0.001$ and $\Delta t = 1.25 \times 10^{-7}$, at various values of t , together with the initial condition (left panel). The total infected $I = I(t)$ are plotted on the right panel. The net reproduction number in this case is $R_0 \approx 4.5$.

We present the solution corresponding to $\bar{r} = 3$, $\eta = 0$, $T = 15$, $\Delta x = 0.001$ and $\Delta t = 1.25 \times 10^{-7}$, at various values of t , together with the initial condition (left panel).

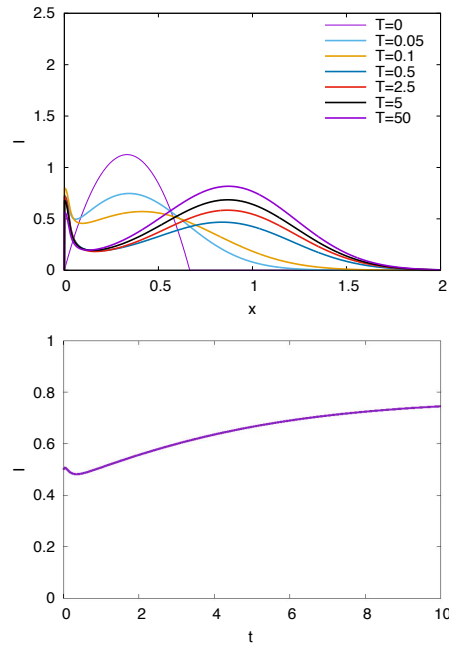


Fig. 1 ^{grid} The case $\bar{r} = 9, \eta = 0$.

{figure1}

The total infected $I = I(t)$ are plotted on the right panel. The net reproduction number was kept just above 4 by changing the parameter α .

We finally present the solution corresponding to $\alpha = 4.8$, $\kappa = 0.3333$, $\bar{r} = 9$, $\eta = 0.01$, $T = 20$, $\Delta x = 0.001$ and $\Delta t = 1.25 \times 10^{-7}$, at $t = 18, 19, 20$ to show stabilization at the equilibrium solution (25), together with the initial condition. The net reproduction number in this case is $R_0 \approx 4.5$.

6 Possible extensions

The model assumes a fixed set of individuals (or patches) and only looks at the distribution of pathogen load (or population) in those. While this may be somewhat rea-

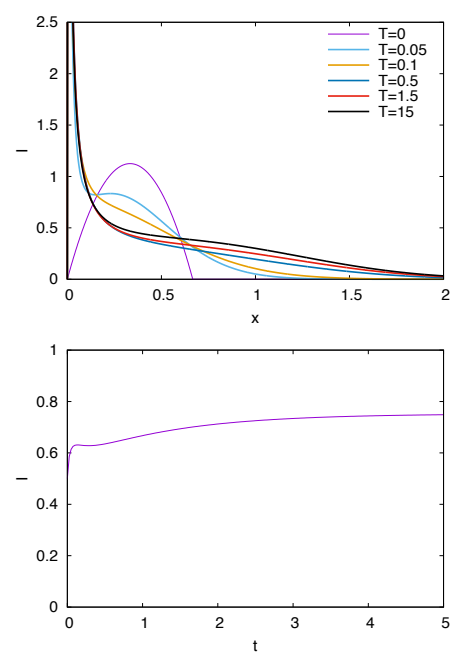
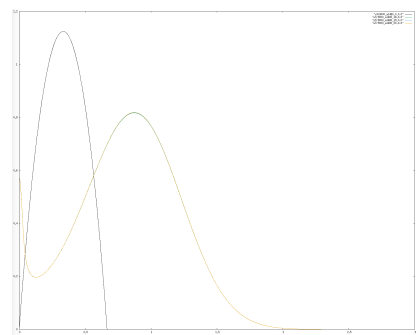


Fig. 2 ^{grid} The case $\bar{r} = 3, \eta = 0$.

{figure2}



{figure3} **Fig. 3** ^{grid} The equilibrium solution with $\alpha = 4.8, \eta = 0.01$.

sonable for patches in metapopulations, it does not make much sense for individuals. One should consider individual births and deaths, and understand how the equation should change.

A simple extension that may be biologically relevant is to assume heterogeneity in individuals (or patches) by attaching an index ω to individuals. From the mathematical point of view, it just means a double integral instead of a single one, however, one may question whether it makes sense to have an infinite population at all values of ω .

Another interesting extension is to assume that $r(x) < 0$ for $x > 0$ small; in other words, a minimum dose is necessary for infection to take over; in the other interpretation, local populations are subject to an Allee effect. We have considered this case computationally here, but not analytically.

One can also add (as is often done in metapopulation models) a catastrophe rate that brings patches instantaneously from size x to 0.

An important extension would be to assume a more complex internal dynamics: infections develop but then are controlled by the immune system; populations grow but then exhaust resources. One could attempt to model this by passing to an (at least) two-dimensional state (x, y) , or giving an age to new infections (colonizations) and letting parameters change with age.

The most complex extension would be to introduce reinfections, i.e. colonizations also of occupied patches: one could assume that emigrants into a patch at level y bring it instantaneously to level $y + x$ with density $q(x)$. This would make it possible to analyze the effect of reinfections (particularly when a minimum dose of infection is necessary for infection success); in metapopulations, this has been called the rescue effect. Mathematically, the problem becomes enormously more complex

because it can no longer be represented as a semilinear equation (perturbation of a well-understood linear differential operator).

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A Appendix

The main step in the proofs of lemmas 1 and 2 is the inequality

$$\int_y^\infty p_0(t, x; \xi) dx = \mathbb{P}(X_t \geq y | X_0 = \xi) \leq \mathbb{P}(X_t \text{ ever reaches } y | X_0 = \xi). \quad (27) \quad \{\mathbf{p_above_x}\}$$

Proof (of Lemma 1) Assuming $L - b > K$, we compute

$$\begin{aligned} \int_L^\infty x^2 p_0(t, x; \xi) dx &= \sum_{n=1}^\infty \int_{L+n-1}^{L+n} x^2 p_0(t, x; \xi) dx \\ &\leq \sum_{n=1}^\infty (L+n)^2 \int_{L+n-1}^\infty p_0(t, x; \xi) dx \\ &= \sum_{n=1}^\infty (L+n)^2 \mathbb{P}(X_t \geq L+n-1 | X_0 = \xi) \\ &\leq \sum_{n=1}^\infty (L+n)^2 \mathbb{P}(X_t \text{ ever reaches } L+n-1 | X_0 = \xi) \\ &= \sum_{n=1}^\infty (L+n)^2 \frac{\int_0^\xi e^{\bar{r}(\zeta-K)^2/(2K)} d\zeta}{\int_0^{L+n-1} e^{\bar{r}(\zeta-K)^2/(2K)} d\zeta} \leq \sum_{n=1}^\infty a_n(L) \end{aligned}$$

with

$$a_n(L) = (L+n)^2 \frac{\int_0^{L-b} e^{\bar{r}(\zeta-K)^2/(2K)} d\zeta}{\int_0^{L+n-1} e^{\bar{r}(\zeta-K)^2/(2K)} d\zeta}.$$

We have

$$\begin{aligned} a_n(L) &\leq (L+n)^3 \\ &\quad \times \frac{\int_0^{L-b} e^{\bar{r}(\zeta-K)^2/(2K)} d\zeta}{(L+n) \int_0^K e^{\bar{r}(\zeta-K)^2/(2K)} d\zeta + \int_K^{L+n-1} (\zeta-K) e^{\bar{r}(\zeta-K)^2/(2K)} d\zeta} \\ &= (L+n)^3 \\ &\quad \times \frac{\int_0^{L-b} e^{\bar{r}(\zeta-K)^2/(2K)} d\zeta}{(L+n) \int_0^K e^{\bar{r}(\zeta-K)^2/(2K)} d\zeta + (K/r) [e^{\bar{r}(L+n-1-K)^2/(2K)} - 1]} \\ &\leq \frac{2\bar{r}}{K} (L+n)^4 e^{(\bar{r}/2K)[(L-b-K)^2 - (L+n-1-K)^2]} \\ &\leq M e^{(\bar{r}/2K)[b(L+n) - 2(L-K)b + b^2 - 2(L-K)(n-1) - (n-1)^2]} \\ &\leq M e^{(\bar{r}/2K)[Kb - b(n-2) - (n-1)^2]} = c_n, \end{aligned}$$

where M is a constant such that $\frac{2\bar{r}}{K} x^4 \leq M e^{\bar{r}bx/(2K)}$ for all $x \geq 0$.

Clearly, $\sum_{n=1}^{\infty} c_n < \infty$. We shall prove next that $\lim_{L \rightarrow \infty} a_n(L) = 0$ for all $n \geq 1$, and then the lemma follows from the dominated convergence theorem.

Using l'Hôpital's rule, we have

$$\begin{aligned} \lim_{L \rightarrow \infty} a_n(L) &= \lim_{L \rightarrow \infty} \frac{2(L+n) \int_0^{L-b} e^{\bar{r}(\zeta-K)^2/(2K)} d\zeta}{e^{(\bar{r}/2K)(L+n-1-K)^2}} \\ &\quad + \lim_{L \rightarrow \infty} (L+n)^2 e^{(\bar{r}/2K)[(L-b-K)^2 - (L+n-1-K)^2]}. \end{aligned}$$

The second limit is equal to

$$\lim_{L \rightarrow \infty} (L+n)^2 e^{-(\bar{r}/2K)(2(L-K)(b+n-1) + (n-1)^2 - b^2)} = 0,$$

and the first one is bounded by $2(L+n)(L-b)e^{(\bar{r}/2K)[(L-b-K)^2 - (L+n-1-K)^2]}$, which also approaches 0 as

$L \rightarrow \infty$.

Proof (of Lemma 2)

Similarly to what we did in the previous proof, we compute

$$\begin{aligned}
 \int_L^\infty x^2 p_0(t, x; \xi) dx &= \int_L^\xi x^2 p_0(t, x; \xi) dx + \sum_{n=1}^\infty \int_{K+(\xi-K)2^{n-1}}^{K+(\xi-K)2^n} x^2 p_0(t, x; \xi) dx \\
 &\leq \xi^2 + \sum_{n=1}^\infty (K + (\xi - K)2^n)^2 \int_{K+(\xi-K)2^{n-1}}^\infty p_0(t, x; \xi) dx \\
 &\leq \xi^2 + \sum_{n=1}^\infty \xi^2 2^{2n} \frac{\int_0^\xi e^{\bar{r}(t-K)^2/(2K)} dt}{\int_0^{K+(\xi-K)2^{n-1}} e^{\bar{r}(t-K)^2/(2K)} dt} \\
 &= \xi^2 \left(1 + \sum_{n=1}^\infty 2^{2n} \frac{\int_0^K e^{\bar{r}cy^2/2} dy + \int_0^{\xi-K} e^{\bar{r}cy^2/2} dy}{\int_0^K e^{\bar{r}cy^2/2} dy + 2^{n-1} \int_0^{\xi-K} e^{\bar{r}cy^2 2^{2(n-1)}/2} dy} \right). \quad (28)
 \end{aligned}$$

Clearly, if we show that the expression in parenthesis is bounded by a positive constant, the lemma is proved.

We compute the derivative with respect to ξ of each term (call it $g_n(\xi)$) in the series in the last line of (28). We obtain

$$\begin{aligned}
 g'_n(\xi) &= \left[I_K \left(e^{v(\xi-K)^2} - 2^{n-1} e^{v(\xi-K)^2 2^{2(n-1)}} \right) \right. \\
 &\quad \left. + 2^{n-1} \int_0^{\xi-K} \left(e^{v(\xi-K)^2 + vy^2 2^{2(n-1)}} - e^{v(\xi-K)^2 2^{2(n-1)} + vy^2} \right) dy \right] / D_n^2
 \end{aligned}$$

where, for the sake of simplicity of notation, we have let $I_K = \int_0^K e^{\bar{r}cy^2/2} dy$, $v = \bar{r}c/2$, and D_n be the denominator of g_n .

It is easy to see that both terms in the expression inside the square brackets for g'_n above are negative, so that g_n is a decreasing function of ξ . Hence, the term in parenthesis in (28) is less or equal than

$$1 + \sum_{n=1}^\infty 2^{2n} \frac{\int_0^K e^{\bar{r}cy^2/2} dy + \int_0^{L-b-K} e^{\bar{r}cy^2/2} dy}{\int_0^K e^{\bar{r}cy^2/2} dy + 2^{n-1} \int_0^{L-b-K} e^{\bar{r}cy^2 2^{2(n-1)}/2} dy},$$

which, in turn, can be bounded by

$$\begin{aligned} & 1 + \sum_{n=1}^{\infty} 2^{2n} \frac{I_K + I_{LbK}}{I_K + 2^{n-1} \int_{(L-b-K)/2}^{L-b-K} e^{\bar{r}cy^2 2^{2(n-1)}/2} dy} \\ & \leq 1 + \sum_{n=1}^{\infty} 2^{2n} \frac{I_K + I_{LbK}}{I_K + 2^{n-2} (L-b-K) (e^{\bar{r}c(L-b-K)^2/8})^{2^{2(n-1)}}}, \end{aligned}$$

where we use the notation I_K and I_{LbK} to represent the integrals with upper limits K and $L-b-K$, respectively. The ratio convergence criterion shows that the last series converges and, therefore, the term in parenthesis in (28) is bounded, and the lemma is proved.

We conclude with the details of the proofs of Propositions 3 and 5.

Proof (of Proposition 3) Take $u_0 \in L_w^1(0, \infty)$ and assume $u_0 \geq 0$ a.e.

We already know that T_t^* is strongly continuous in $L^1(0, \infty)$; hence, we only need to show that

$$\lim_{t \rightarrow 0^+} \int_0^\infty x^2 \left| \int_0^\infty u_0(\xi) p_0(t, x; \xi) d\xi - u_0(x) \right| dx = 0. \quad (29)$$

Let $\varepsilon > 0$ and $b > 0$ be arbitrary, and find $L > 0$ such that

$$\int_{L-b}^\infty x^2 u_0(x) dx < \frac{\varepsilon}{3(C+1)},$$

where C is the constant from Lemma 2 (such L exists because $u_0 \in L_w^1(0, \infty)$), and also (see Lemma 1)

$$\sup_{0 < \xi \leq L-b} \int_L^\infty x^2 p_0(t, x; \xi) dx < \frac{\varepsilon}{3\|u_0\|_1}.$$

Next, let $h > 0$ be such that

$$\int_0^\infty \left| \int_0^\infty u_0(\xi) p_0(t, x; \xi) d\xi - u_0(x) \right| dx < \frac{\varepsilon}{3L^2}$$

for all $0 < t \leq h$, whose existence follows from the strong continuity of T_t^* in $L^1(0, \infty)$.

Then,

$$\begin{aligned}
& \int_0^\infty x^2 \left| \int_0^\infty u_0(\xi) p_0(t, x; \xi) d\xi - u_0(x) \right| dx \\
&= \int_0^L x^2 \left| \int_0^\infty u_0(\xi) p_0(t, x; \xi) d\xi - u_0(x) \right| dx \\
&\quad + \int_L^\infty x^2 \left| \int_0^\infty u_0(\xi) p_0(t, x; \xi) d\xi - u_0(x) \right| dx \\
&\leq L^2 \int_0^\infty \left| \int_0^\infty u_0(\xi) p_0(t, x; \xi) d\xi - u_0(x) \right| dx \\
&\quad + \int_L^\infty x^2 \int_0^\infty u_0(\xi) p_0(t, x; \xi) d\xi dx + \int_L^\infty x^2 u_0(x) dx \\
&\leq \frac{\varepsilon}{3} + \int_0^{L-b} u_0(\xi) \int_L^\infty x^2 p_0(t, x; \xi) dx d\xi \\
&\quad + \int_{L-b}^\infty u_0(\xi) \int_L^\infty x^2 p_0(t, x; \xi) dx d\xi + \frac{\varepsilon}{3(C+1)} \\
&\leq \frac{\varepsilon}{3} + \frac{\varepsilon}{3} \int_0^{L-b} u_0(\xi) d\xi + C \int_{L-b}^\infty u_0(\xi) \xi^2 d\xi + \frac{\varepsilon}{3(C+1)} \leq \varepsilon.
\end{aligned}$$

For a general u_0 , write $u_0 = u_0^+ - u_0^-$ and apply the previous result to u_0^+ and u_0^- .

Proof (of Proposition 5) For $t \in [0, T]$, let

$$\lambda(t) = \int_0^\infty \beta(x) u(t, x) dx.$$

We shall argue by contradiction. Since $\lambda(0) > 0$, by continuity it follows that $\lambda(t) > 0$ for t small; thus we define

$$\tau = \inf\{t \in [0, T] : \lambda(t) < 0\}.$$

This is just saying that τ is the first positive time at which u vanishes. On $[0, \tau]$ the solution u of (14) can be written probabilistically as the density function of a process Y_t , a variation of the elementary return process introduced by (Feller, 1954). Following the construction used by (Peng and Li, 2013) (in a much simpler case than the original), we write $u(t, \cdot)$ explicitly as the transition probability function for Y_t using simple ingredients. In fact, although all terms may be interpreted probabilistically, we shall just build the needed ingredients for our construction of the solution.

Let

$$A(t, \xi) = 1 - \int_0^\infty p_0(t, x; \xi) dx > 0 \tag{30} \quad \{\mathbf{q}\}$$

be the probability that process X_t is absorbed at $x = 0$ before time $t > 0$ conditional on $X_0 = \xi$, and let

$$\bar{A}(t) = \int_0^\infty A(t; \xi) q(\xi) d\xi$$

represent the absorption probability if the initial distribution is q .

Let

$$E_0 = 1 - \int_0^\infty u_0(x) dx \geq 0,$$

and define, for $t > 0$,

$$F_1(t) = \int_0^\infty A(t; \xi) u_0(\xi) d\xi + E_0 \int_0^t \lambda(s) e^{-\int_0^s \lambda(u) du} \bar{A}(t-s) ds. \quad (31)$$

F_1 can be interpreted as the probability that the process Y_t gets absorbed at least once by time t .

As F_1 is continuous and increasing, we can consider its derivative $f_1 = F_1'$ and—to simplify notation—we consider $F_1(t) = \int_0^t f_1(s) ds$, which is presumably true; if not, one should simply read $f_1(t) dt$ as $dF_1(t)$ and similarly for $f_n(t)$ defined below.

We then define iteratively the function $F_n, n \geq 1$, as

$$F_n(t) = \int_0^t f_{n-1}(s) \int_s^t \lambda(u) e^{-\int_s^u \lambda(v) dv} \bar{A}(t-u) du ds. \quad (32)$$

From (32), as \bar{A} is a non-decreasing function, we derive the following bound for any $t \leq T$:

$$\begin{aligned} F_n(t) &\leq \int_0^t f_{n-1}(s) \int_s^t \lambda(u) e^{-\int_s^u \lambda(v) dv} \bar{A}(t-s) du ds \\ &= \int_0^t f_{n-1}(s) \left(1 - e^{-\int_s^t \lambda(v) dv}\right) \bar{A}(t-s) ds \leq \rho F_{n-1}(t) \end{aligned} \quad (33)$$

with

$$\rho = \left(1 - e^{-\int_0^T \lambda(v) dv}\right) \bar{A}(T) < 1. \quad (34)$$

This ensures that the series $\sum_{n=1}^\infty F_n$ converges uniformly on $[0, T]$.

Now let us define

$$E(t) = E_0 \exp\left\{-\int_0^t \lambda(v) dv\right\} + \sum_{n=1}^\infty \int_0^t f_n(s) \exp\left\{-\int_s^t \lambda(v) dv\right\} ds, \quad (35)$$

and

$$\begin{aligned} u(t, x) &= \int_0^\infty u_0(\xi) p_0(t, x; \xi) d\xi \\ &+ E_0 \int_0^t \lambda(s) e^{-\int_0^s \lambda(v) dv} \int_0^\infty q(\xi) p_0(t-s, x; \xi) d\xi ds \\ &+ \sum_{n=1}^\infty \int_0^t f_n(s) \int_s^t \lambda(u) e^{-\int_s^u \lambda(v) dv} \int_0^\infty q(\xi) p_0(t-u, x; \xi) d\xi du ds \\ &= \int_0^\infty u_0(\xi) p_0(t, x; \xi) d\xi + \int_0^t \lambda(s) E(s) \int_0^\infty q(\xi) p_0(t-s, x; \xi) d\xi ds. \end{aligned} \quad (36)$$

We wish to prove that $u(t, x)$ is, in fact, an explicit form of the solution to (14). By construction, it is clear that both E and u are positive. Moreover, we have

$$\begin{aligned}
\int_0^\infty u(t, x) &= \|u_0\|_1 - \int_0^\infty u_0(\xi) A_0(t, \xi) d\xi + E_0 \left(1 - e^{-\int_0^t \lambda(v) dv} \right) \\
&\quad - E_0 \int_0^t \lambda(s) e^{-\int_0^s \lambda(v) dv} \bar{A}(t-s) ds \\
&\quad + \sum_{n=1}^\infty \int_0^t f_n(s) \left(1 - e^{-\int_s^t \lambda(v) dv} \right) ds \\
&\quad - \sum_{n=1}^\infty \int_0^t f_n(s) \int_s^t \lambda(u) e^{-\int_s^u \lambda(v) dv} du ds \\
&= \|u_0\|_1 + E_0 - \int_0^t f_1(s) ds - E(t) \\
&\quad + \sum_{n=1}^\infty \int_0^t f_n(s) ds - \sum_{n=1}^\infty \int_0^t f_{n+1}(s) ds,
\end{aligned}$$

the last step coming from (32). Hence we have obtained

$$\|u(t)\|_1 = 1 - E(t) \quad \text{for all } t \in [0, \tau],$$

where $E(\cdot) > 0$ is defined through (35). Thus, we have proved $\|u(\tau)\|_1 < 1$. Finally, from the last line of (36), it is easy to see that

$$u_t(t, x) = \partial_x \left[(a(x)u(t, x))_x - r(x)u(t, x) \right] + \lambda(t)E(t)q(x),$$

with $E(t) = 1 - \|u(t)\|_1$, and thus u is indeed the solution of (14).

Since $u(\cdot) \geq 0$ and λ was defined as

$$\lambda(t) = \int_0^\infty \beta(x)u(t, x) dx,$$

we have obtained a contradiction with $\tau = \inf\{t \in [0, T] : \lambda(t) < 0\}$.

Hence (36) holds for all $t \in [0, T]$, and we have established that $u(t) \geq 0$ and $\|u(t)\|_1 < 1$ on this interval.