STRUCTURED POPULATIONS
WITH DIFFUSION IN STATE SPACE

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Dedicated to Horst R. Thieme on the Occasion of his 60th Birthday

ABSTRACT. The classical models for populations structured by size have two features which may cause problems in biologically realistic modeling approaches: the structure variable always increases, and individuals in an age cohort that are identical initially stay identical throughout their lives. Here a diffusion term is introduced in the partial differential equation which mathematically amounts to adding viscosity. This approach solves both problems but it requires to identify appropriate boundary (recruitment) conditions. The method is applied to size-structured populations, metapopulations, infectious diseases, and vector-transmitted diseases.

1. **Introduction.** The present paper is about how to introduce diffusion in size structure models, i.e., about diffusion in size space. Hence we work with convection diffusion equations and suitable boundary conditions and we neglect technical difficulties that may arise for certain classes of problems, notably in unbounded domains.

Suppose we have a population which is structured by some character x, a non-negative real number. Then we can describe the state of the population by its density $u(x) \geq 0$ such that $\int_{x_1}^{x_2} u(x)dx$ defines that part of the population which has its character in the interval $[x_1, x_2)$. The standard examples are populations structured by age or by size which are governed by a scalar first order partial differential equation

$$u_t + (g(x)u)_x = 0 \qquad (1)$$

together with a boundary condition at $x = 0$ describing recruitment.

For x being chronological age such models were used already by Daniel Bernoulli around 1760 (neglecting the birth process), cast into the form of renewal equations by Sharpe and Lotka around 1910, and into the form of partial differential equations by McKendrick 1926. The renewal theorem was proved by Feller in 1941. The application to size structure goes back at least to Sinko and Streifer 1967. Gurtin and MacCamy 1974 allowed birth and death rates to depend on total population density.

For these biological models mathematical theories have been developed. This has been necessary as these problems are far from the standard problems of mathematical physics. The difference can be explained at the level of matrices. Mathematical physics uses mostly self-adjoint operators in L_2 spaces (symmetric matrices with a complete set of eigenvectors) while population dynamics uses extremely non-symmetric operators in L_1 spaces (corresponding to Frobenius companion or Leslie matrices which have only one eigenvector for each eigenvalue).

The mathematical theory, based on (integrated) semigroups or the sun-star technology culminates in the subjunction of practically "all" population models into a system of a delay equation and a mapping. Indeed, some classical examples of delay equations can be best motivated as limiting cases of population models with age structure, and for neutral delay equations this seems to be the only way of a rigorous derivation.

There are rather general models with parameters depending on size and total population such as given in [2],

$$u_t + (g(x, P(t))u)_x + \mu(x, P(t))u = 0$$

$$g(0, P(t))u(t, 0) = \int_0^\infty b(x, P(t))u(t, x)dx.$$

These models are perfect as long as the structure variable x is age since indeed everybody ages by one year when time proceeds by one year.

With respect to size these models appear less justified since two problems arise. According to the model (1) the size of each individual follows the characteristic differential equation

$$\dot{x} = g(x) \tag{2}$$

while in reality there is quite some variation in size between individuals of the same cohort. If the character x describes a quantity that can increase and decrease, like body fat in mammals or birds, then the convection rate changes sign and solutions tend to build up peaks.

Introducing diffusion in the state space (which in general is not physical space) solves both problems. On the modeling side diffusion incorporates stochastic effects in a deterministic framework and allows variation within cohorts. On the mathematical side introducing diffusion corresponds to a viscosity approach in hyperbolic equations. It leads to parabolic (instead of hyperbolic) equations and the existence and regularity problems become much easier, even when characteristic curves change direction. But the viscosity approach needs boundary conditions. These cannot be derived from the differential equations but must be supplied by the underlying physical or biological problem. Indeed, much of the following amounts to discussions of boundary conditions.

The idea to supply state structured population models or epidemic models with a diffusion term is not new, see [11] and more recently [10] (following [8] [9]) and [7] for models for host-parasite populations. However, [11] as well as some more recent versions leave questions open with respect to the transition between individuals with a low level of infection and completely infection-free individuals. One has tried to answer these questions by introducing a minimal dose of infection, i.e., study the problem on $(1, \infty)$ rather than on $(0, \infty)$. But this shift seems not to be a remedy to the problem of choosing the "right" boundary condition. To some extent the choice of the boundary condition and of the recruitment law is a modeling problem and not a mathematical problem. Here the modeler's views enter about how parasites invade

hosts and how hosts get cured from infection. The answer will depend on whether one models helminth parasites or bacteria and virus and whether superinfection plays some role. Here we do not give an ultimate answer to these problems but we suggest and explain modeling approaches for various scenarios.

Our applications concern populations structured by size x, metapopulations of colonies of size x, epidemic models where the infected are structured by the level of infection or severity of illness x, macroparasite models (schistomiasis, onchocercasis) where x is the number of parasites within the human body, treated as a continuous variable. There may be applications to populations of individuals having assets x that can go up and down and show volatility. In many of these applications it will be necessary (from a modeling point of view) to have an "empty" compartment of empty habitats or uninfected hosts.

2. **Structured populations.** The first order convection equation (1), on the interval $[0, \infty)$, describes a population structured by some variable $x \geq 0$. We consider non-negative integrable solutions $u(t, x)$.

We imagine that the function g is extended to a continuously differentiable function (with the same name g) on $(-\infty, \infty)$ and that the solutions of the characteristic differential equation (2) exist for all initial data $x(0) = x_0$ and for all times $-\infty < t < \infty$. Let $G(t, x)$ be the solution operator of the equation (2), i.e.,

$$\frac{d}{dt}G(t, x) = g(G(t, x)), \quad G(0, x) = x.$$

Suppose we have an initial condition $u(0, x) = u_0(x)$ for the equation (1). Then we find the solution as

$$u(t, x) = e^{-\int_0^t g'(G(-s, x))ds} u_0(G(-t, x)). \tag{3}$$

Indeed g' appears in the exponent and not just g. If g is a positive function then then this expression is the same as

$$u(t, x) = \frac{g(G(-t, x))u_0(G(-t, x))}{g(x)}. \tag{4}$$

We distinguish several cases.

i) If $g(0) > 0$ then the half-line $[0, \infty)$ is positively invariant with respect to the flow of (2). If we want to study a equation (1) on the half-line $[0, \infty)$ then we have to prescribe a boundary condition at $x = 0$. Then the characteristic curve $x = G(t, 0)$ separates two wedge domains in R_+^2. For $x > G(0, t)$ the solution is determined by the initial data, for $x < G(t, 0)$ the solution is determined by the boundary data.

If the structure variable is size ($g(x) > 0$) or age ($g = 1$) then the natural boundary condition is a recruitment law

$$g(0)u(t, 0) = N(t) \tag{5}$$

where $N(t)$ is the recruitment (birth) rate.

ii) If $g(0) = 0$ then $x = 0$ is a stationary point of (2). Again the half-line is positively invariant with respect to the flow of (2). We find $u(t, 0) = \exp\{-g'(0)t\}u_0(t, 0)$. We cannot prescribe a boundary condition.

iii) If $g(0) < 0$ then the value $u(t, 0)$ is determined by the initial data in $(0, \infty)$ as

$$u(t, 0) = e^{-\int_0^t g'(G(-s,0))ds} u_0(G(-t, 0)). \tag{6}$$

Since $G(-t, 0) > 0$ we see that values of the initial data are transported from $x > 0$ to $x = 0$. We cannot prescribe a boundary condition at $x = 0$. The behavior of the function g for $x > 0$ (sign changes etc.) does not matter. It is only the sign of $g(0)$ that counts.

Typical examples are x being a resource that is depleted or a level of infection that decreases at a rate $\sigma(x) \geq 0$. To stay within the framework of equation (1), we put $\sigma(x) = -g(x)$.

The differences between the three cases are basic: they show up in any modeling attempt for structured populations.

We introduce diffusion in equation (1) and get a convection diffusion equation

$$u_t + (g(x)u)_x = (D(x)u_x)_x \tag{7}$$

with a diffusion coefficient $D(x) > 0$. As a biological model, equation (7) describes growth or depletion with some stochastic variation.

Now we need a boundary condition at $x = 0$ whatever the sign of $g(0)$ is, and there is no way to *derive* the boundary condition from the equation (7) or from the previous boundary conditions (5) or (6).

For the equation (7) the flux at $x = 0$ is

$$- D(0)u_x(t, 0) + g(0)u(t, 0). \tag{8}$$

If we think of a reaction in a test tube then a no-flux boundary condition

$$- D(0)u_x(t, 0) + g(0)u(t, 0) = 0 \tag{9}$$

may seem appropriate. Of course it ensures conservation of mass (for solutions that decay fast for $x \to \infty$).

But if we think of the equation (1) as a model for a size-structured population then the flux at $x = 0$ is given by (5), and introducing some noise should not drastically change the recruitment law. Hence a boundary condition

$$- D(0)u_x(t, 0) + g(0)u(t, 0) = N(t) \tag{10}$$

seems more appropriate. In biological terms the condition says that the true flux through the boundary is equal to the function $N(t)$ (whereby $N(t)$ will be derived from some birth law).

We could also assume that the recruitment law is "deterministic" in the sense that the boundary condition for equation (7) is given by equation (5).

These two choices are just special cases of a general boundary condition of Robin type

$$- cD(0)u_x(t, 0) + g(0)u(t, 0) = N(t) \tag{11}$$

with $c \in [0, 1]$. The limiting cases $c = 1$ and $c = 0$ correspond to (10) and (5). Any choice of c is mathematically correct and also justified from a biological point of view. Different choices of c reflect the modeler's view on how recruitment works.

Notice that for $D(0) \to 0$ each of the boundary conditions (11) reduces to (5) which again underlines that there is no preferred condition.

To see the effects of different choices of the parameter c we consider a problem with constant coefficients

$$u_t + gu_x = Du_{xx} - \mu u, \quad -cDu_x + gu = b \int_0^\infty u dx. \tag{12}$$

We look for an exponential solution $u(t, x) = \exp\{-\sigma x + \lambda t\}$. We find

$$D\sigma^2 + g\sigma = \lambda + \mu, \quad cD\sigma + g = \frac{b}{\sigma}$$

and hence

$$\sigma(c) = \frac{g}{2cD}\left(\sqrt{1 + 4\frac{bcD}{g^2}} - 1\right), \quad \lambda(c) = D\sigma^2 + g\sigma - \mu$$

with $\sigma(0) = b/g$. As c runs downward from $c = 1$ to $c = 0$, the exponent increases from $\lambda(1) = b - \mu$ to $\lambda(0) = b - \mu + D(b/g)^2$. Hence the modified boundary condition with $c < 1$ leads to increased population growth.

The same insight can be gained from the changes in total population size. From (12) it follows that

$$\frac{d}{dt}\int_0^\infty u(t, x)dx = (b - \mu)\int_0^\infty u(t, x)dx - (1 - c)Du_x(t, 0).$$

The last term describes the change due to the boundary condition. Of course $u_x(t, 0)$ depends on the other parameters.

Now suppose $g(0) \leq 0$. The equation (1) does not allow a boundary condition. What boundary condition should we choose for the equation (7)? In the case $g(0) > 0$ we had equated the flux (8) of the convection-diffusion equation to the flux of the equation (1), i.e., the recruitment term, to get (10). We propose to do the same here (not considering the more general case with a parameter c). We set the flux (8) equal with the flux of the equation (1) which is $g(0)u(t, 0)$. Then we get the the boundary condition

$$-D(0)u_x(t, 0) + g(0)u(t, 0) = g(0)u(t, 0) \tag{13}$$

which is

$$-D(0)u_x(t, 0) = 0. \tag{14}$$

Hence it appears that (14) is the most appropriate condition in the case $g(0) \leq 0$. For $D(0) \to 0$ this condition becomes void, as it should be, since we cannot prescribe a boundary condition for the equation (1).

Although (14) would be a reflecting boundary condition for the heat equation, it is not a reflecting condition for the convection diffusion equation with $g(0) < 0$. Further notice that a no-flux condition $-D(0)u_x(t, 0) + g(0)u(t, x) = 0$ would not be appropriate since the differential equation indeed moves mass through the boundary, unless $g(0) = 0$.

In more complex modeling problems the function g will depend on t via the (unknown) solution $u(t, x)$ and will change sign at unknown times. Hence we look at the situation where $g(0)$ (depending on other parameters) may change sign. Then the boundary condition with $c = 1$ becomes

$$-D(0)u_x(t, 0) + g(0)u(t, 0) = \begin{cases} N(t) & g(0) > 0 \\ g(0)u(t, 0) & g(0) \leq 0 \end{cases} \tag{15}$$

with the assumption that $N(t) = 0$ if $g(0) \leq 0$. Of course, if one starts with any initial data and and prescribed boundary data $N(t)$ then the right hand side may become discontinuous. In an actual population model the function $N(t)$ goes to zero when $g(0)$ approaches zero from above.

In [10] [7] a parasite host model has been designed which fits into the present framework. In this model hosts are structured with respect to the parasite level x. There are no totally uninfected hosts but just hosts with parasite level $x = 0$. Consequently, the authors use a no flux boundary condition. In our language the model equations read

$$u_t + (g(t, x)u)_x = (D(x)u_x)_x - \mu(x)u$$
$$-D(0)u_x(t, 0) + g(t, 0)u(t, 0) = 0 \tag{16}$$

with

$$g(t, x) = \left(\rho \frac{\int_0^\infty u(t, x)dx}{1 + \int_0^\infty u(t, x)dx} - \nu \right) x.$$

Here $\mu(x)$ is the host mortality and ν is the parasite mortality. The convection rate g may change sign but in view $g(t, 0) \equiv 0$ the boundary condition is not affected.

3. **Introducing an empty compartment.** Now we introduce an "empty" time-dependent compartment U (representing uninfected individuals or empty colonies) and try to derive a system of the general form

$$U_t = \cdots$$
$$u_t + (g(x)u)_x = (D(x)u_x)_x + \cdots$$
$$-D(0)u_x(t, 0) + g(0)u(t, 0) = \cdots$$

Again we look first at the case $g(0) > 0$. Individuals may leave the U compartment and enter the u compartment at any level x or enter the u compartment at the boundary. Let $\psi(x)$ be the transition rate. If we require conservation of mass then we get a system of the form

$$U_t = - \int_0^\infty \psi(x)dx\, U - N(t)$$
$$u_t + (g(x)u)_x = (D(x)u_x)_x + \psi(x)U$$
$$-D(0)u_x(t, 0) + g(0)u(t, 0) = N(t). \tag{17}$$

The conservation argument does *not* tell what the function $N(t)$ is. The quantity $N(t)$ is the rate (per time) at which individuals leave the U compartment and enter the u compartment at $x = 0$. If we take the view that the transition is entirely deterministic (as in (10), corresponding to $c = 1$ above) then we get the system

$$U_t = - \int_0^\infty \psi(x)dx\, U - N(t)$$
$$u_t + (g(x)u)_x = (D(x)u_x)_x + \psi(x)U$$
$$-D(0)u_x(t, 0) + g(0)u(t, 0) = N(t). \tag{18}$$

We can assume that there is no transition at all at $x = 0$. Then any individual leaving U for u arrives with a positive level x and the level $x = 0$ is reached only

by diffusion from positive values x. Then we have the system

$$U_t = -\int_0^\infty \psi(x)dx\, U$$

$$u_t + (g(x)u)_x = (D(x)u_x)_x + \psi(x)U$$

$$-D(0)u_x(t,0) + g(0)u(t,0) = 0. \tag{19}$$

The situation where $g(x)$ is positive corresponds to an immigration-birth or growth process within the u compartment. In terms of infection by parasites, an immigration-death process seems more realistic. Then we get, instead of (19), with $\sigma(x) = -g(x)$,

$$U_t = -\int_0^\infty \psi(x)dx U + \sigma(0)u(t,0)$$

$$u_t - (\sigma(x)u)_x = (D(x)u_x)_x + \psi(x)U$$

$$-D(0)u_x(t,0) = 0. \tag{20}$$

Here we assume that individuals leave the empty compartment and enter the occupied compartment at any level x but they leave the occupied compartment only at $x = 0$. For constant coefficients $D, g, \sigma > 0$ and

$$\psi(x) = \tau e^{-\tau x} \tag{21}$$

we find the equilibrium solution $U = 1$,

$$u(x) = \begin{cases} \frac{1}{\sigma - \tau D}\left(e^{-\tau x} - \frac{D\tau}{\sigma}e^{-(\sigma/D)x}\right) & \sigma \neq \tau D \\ \left(\frac{x}{D} + \frac{D}{\sigma}\right)e^{-(\sigma/D)x} & \sigma = \tau D. \end{cases} \tag{22}$$

In this case the function u is decreasing.

4. **Metapopulation models.** We apply the ideas to metapopulation models. Let $U(t)$ be the density of empty habitats and let $u(t,x)$ be the density of occupied habitats with colony size x.

Let $g(x)$ with $g(0) \geq 0$ describe the intrinsic dynamics of colonies, let $D(x)$ be the volatility (diffusion rate). Let $\mu(x)$ be the rate of colony extinction due to random catastrophes.

A colony of size x produces colonizing individuals at a rate $b(x)$. Let ψ_0 be the rate at which an empty habitat takes colonists, and let $\psi(x)$ the uptake rate into a colony of size x. Then we can formulate a model as follows,

$$u_t + (g(x)u)_x = (D(x)u_x)_x - \mu(x)u + \psi(x)UN(t), \tag{23}$$

$$-D(0)u_x(t,0) + g(0)u(t,0) = 0, \tag{24}$$

$$U_t = \int_0^\infty \mu(x)u(t,x)dx - \int_0^\infty \psi(x)dx\, UN(t) \tag{25}$$

where

$$N(t) = \int_0^\infty b(x)u(t,x)dx.$$

We have conservation of mass

$$\frac{d}{dt}\left(U(t) + \int_0^\infty u(t,x)dx\right) = 0.$$

We assume that the total mass is normalized to 1.

This is not a linear model. There is a mass action kinetics term UN and hence there is a critical condition for persistence of the population.

The case of constant coefficients tells how this model system behaves. We assume that D, g, μ, b are positive constants and that $\psi(x)$ is a non-negative function with $\int_0^\infty \psi(x)dx = \bar{\psi} > 0$. We define $\bar{u}(t) = \int_0^\infty u(t,x)dx$.

Then $N = b\bar{u}$ and the system becomes

$$
\begin{aligned}
u_t + gu_x &= Du_{xx} - \mu u + \psi(x)bU\bar{u} \\
U_t &= \mu\bar{u} - \bar{\psi}bU\bar{u} \\
-Du_x(0) + gu(0) &= 0.
\end{aligned}
$$

We integrate over x and get

$$
\begin{aligned}
\bar{u}_t &= -\mu\bar{u} + \bar{\psi}bU\bar{u} \\
U_t &= \mu\bar{u} - \bar{\psi}bU\bar{u}
\end{aligned}
$$

and finally

$$
\bar{u}_t = -\mu\bar{u} + \bar{\psi}b\bar{u}(1 - \bar{u}). \tag{26}
$$

The equation (26) is a modified Verhulst equation. The population persists if the inequality

$$
\frac{\bar{\psi}b}{\mu} > 1 \tag{27}
$$

is satisfied. We may call the left hand side a basic reproduction number R_0.

The threshold condition (27) says that the population can persist if the product of individual birth rate b and mean colonization rate $\bar{\psi}$ exceeds the rate of random catastrophes μ. In this simple case R_0 does not depend on D, g and the specific choice of the function ψ. In the general case one can proceed as follows. Linearize the system at the constant solution $(u, U) = (0, 1)$. We call the variables again u and U. The linearized system reads

$$
\begin{aligned}
u_t &= (D(x)u_x)_x - (g(x)u)_x - \mu(x)u + \psi(x)\int_0^\infty b(x)udx \\
U_t &= \int_0^\infty \mu(x)udx - \int_0^\infty \psi(x)dx \int_0^\infty b(x)udx \\
&\quad -D(0)u_x(t,0) + g(0)u(t,0) = 0.
\end{aligned}
$$

The population persists if the corresponding eigenvalue problem has a positive eigenvalue. Since the right hand side of the U equation does not depend on U we need only consider the u equation. We find that the population persists if the eigenvalue problem

$$
\begin{aligned}
(D(x)u_x)_x - (g(x)u)_x - \mu(x)u + \psi(x)\int_0^\infty b(x)udx &= \lambda u \\
-D(0)u_x(0) + g(0)u(0) = 0, \quad u &\in L^1(0, \infty) \tag{28}
\end{aligned}
$$

has a positive eigenvalue λ.

5. **Epidemic models.** In standard epidemic models the population is subdivided into classes like susceptible, vaccinated, exposed, infectious, recovered etc., but in most cases the level of infection or the severity of the illness is not described. Exceptions are macroparasite models of the Kostizyn type where the hosts of a helminth parasite are classified by the number of adult parasites they carry. The idea to design, study and apply similar models for a continuous variable which describes the individual level of infection has been around for some time [11] but has been only recently further developed [8] [9] [10].

Consider an SIR(S) model with susceptible S, infected I, and recovered R whereby the infected are structured by the level of infection $x \geq 0$. The density of infected is $u(t, x)$. The total number of infected is $I = \int_0^\infty u dx$.

The parameter $\beta(x)$ is the infectivity of an infected individual with level of infection x. The dynamics of the disease within an infected individual is described by a convection rate $g(x)$ (decay or growth of the parasite population), a diffusion rate $D(x)$ (stochastic variation of the parasite population), and the rate $\alpha(x)$ of complete recovery. The density $\psi(x) \geq 0$, $\int_0^\infty \psi(x) dx = 1$, describes the initial level of infection once a susceptible individual becomes infected.

The model is given by the following equations:

$$\dot{S} = -w + \gamma R \tag{29}$$

$$w = S \int_0^\infty \beta(x) u(t, x) dx \tag{30}$$

$$u_t + (g(x)u)_x = (D(x)u_x)_x - \alpha(x)u + \psi(x)w \tag{31}$$

$$- D(0)u_x(t, 0) + g(0)u(t, 0) = 0 \tag{32}$$

$$\dot{R} = \int_0^\infty \alpha(x) u(t, x) dx - \gamma R. \tag{33}$$

This model system is meaningful whatever the sign of $g(0)$ is. Notice that, generally speaking, $g(x) \leq 0$ corresponds to a disease where parasites within a host are governed by an immigration-death process (as in helminth infections) whereas $g(x) \geq 0$ describes parasites which multiply within the host (bacteria, virus).

The threshold condition assumes the form of an eigenvalue problem (compare (28))

$$(D(x)u_x)_x - (g(x)u)_x + \psi(x) \int_0^\infty \beta(x)u(x)dx - \alpha(x)u = \lambda u$$
$$-D(0)u_x(t, 0) + g(0)u(t, 0) = 0, \quad u \in L_1(0, \infty). \tag{34}$$

The uninfected state is unstable if there is a positive eigenvalue λ. It is not evident how an explicit formula for the basic reproduction number would look like.

If β and α are constant, then the variables S, I, R satisfy the system

$$\begin{aligned}
\dot{S} &= -\beta SI + \gamma R \\
\dot{I} &= \beta SI - \alpha I \\
\dot{R} &= \alpha I - \gamma R
\end{aligned}$$

whatever the functions g and D are.

Consider the case of constant coefficients, $g > 0$, with ψ as in (21).

We look for stationary distributions. We fix $w = 1$ and ask for u satisfying the differential equation and the boundary condition. We find (for $D\tau^2 + g\tau - \alpha \neq 0$, compare (22))

$$u(x) = \frac{\tau}{D\tau^2 + g\tau - \alpha} \left[\frac{2(D\tau + g)}{\sqrt{g^2 + 4\alpha D} + g} e^{-x(\sqrt{g^2 + 4\alpha D} - g)/(2D)} - e^{-x\tau} \right]. \tag{35}$$

This formula can be used in several ways. In the case of an SIR model ($\gamma = 0$) the asymptotic distribution of infected is given by $u(x)\phi(t)$ where $\phi(t)$ is an eventually decaying time-dependent factor. In the case of an SIRS model the formula represents the (non-normalized) distribution of infected individuals at equilibrium.

6. **Models for vector-borne disease.** With respect to vector-borne diseases we
have a look at an earlier paper [11] which followed the example of Kostizyn [4]
models for macroparasite infection that had been extensively studied in [5] [6] [3].
With very few exceptions, helminth parasites do not multiply in the host. On the
other hand, superinfection is frequent. Hence we have to implement the transition
from uninfected to infected and superinfection within the infected population. If
there is no (super-)infection then the parasite population within an individual host
decreases.

The uninfected hosts are represented by the compartment $U(t)$ and infected hosts
by the density $u(t, x)$. The parasite load in the environment is $w(t)$, and φ is the
infected force exerted by the (infected) vector population or simply an immigration
rate of parasites.

An uninfected individual may become infected by x parasites and thus enter the
infected class at level x. The function $\psi(x)$ determines the distribution of these
newly infected individuals with respect to x. Superinfection can be modeled by
a kernel describing jumps from y to $x > y$ parasites within an individual or by a
convection term, with parameter $\phi(x)$, driven by the infective force. The death rate
of parasites within the host is $\sigma(x)$ and stochastic variation is implemented by the
diffusion rate $D(x)$. We include a recovery rate $\alpha(x)$ which, seen from the parasite
population within a host, is the rate of catastrophic extinction.

It seems reasonable to assume $\sigma(0) = 0$. But this assumption implies that an
infected individual does never return to the class U. Hence we allow $\sigma(0) \geq 0$ and
enter an appropriate term in the U equation. In view of the definition of primary
infection and superinfection we must require $\phi(0) = 0$. Then we get a system with
a simple boundary condition,

$$U_t = -\int_0^\infty \psi(x)dx\varphi(t)U + \sigma(0)u(t,0) + \int_0^\infty \alpha(x)u(t,x)dx \tag{36}$$

$$u_t - (\sigma(x)u)_x + \varphi(t)(\phi(x)u)_x = (D(x)u_x)_x - \alpha(x)u + \psi(x)\varphi(t)U \tag{37}$$

$$-D(0)u_x(t,0) = 0 \tag{38}$$

$$\varphi(t) = \beta f(w(t)) \tag{39}$$

$$w(t) = \frac{\int_0^\infty xu(t,x)dx}{U(t) + \int_0^\infty u(t,x)dx}. \tag{40}$$

The model differs from (16) in several aspects. First of all, there is a compartment
of uninfected U. Therefore the no flux condition is not the only possible boundary
condition at $x = 0$. Then the immigration law is different and, because it makes
use of the average number of parasites in all hosts, it is perhaps closer to the law in
the discrete model [5]. In [6] the model with discrete parasites has been compared
to the model from [1] for interacting host and parasite populations with a given
clumped distribution of parasites within hosts. The present model appears as an
intermediate case.

As in the previous section we look at an example with constant coefficients. We
must assume $\phi = 0$. We choose ψ as in (21) and, to keep things simple, we assume
$\alpha = 0$,

$$U_t = -\varphi(t)U + \sigma u(t,0) \tag{41}$$

$$u_t - \sigma u_x + \varphi(t)\psi u_x = Du_{xx} + \tau e^{-\tau x}\varphi(t)U, \tag{42}$$

the other equations remain the same.

For the parasite distribution within hosts we find (compare (35))

$$u(x) = \varphi U \frac{\tau}{\sigma - D\tau} \left(\frac{1}{\tau} e^{-\tau x} - \frac{D}{\sigma} e^{-(\sigma/D)x} \right). \tag{43}$$

The mean parasite load is

$$w = \frac{(\sigma + D\tau)\varphi}{\sigma^2\tau + (\sigma + D\tau)\varphi}. \tag{44}$$

We find: The mean parasite load increases with the immigration rate φ, and it decreases with parasite death rate σ. The mean parasite load is an increasing function of D and a decreasing function of τ. For $\alpha > 0$ we get the same result, the formulas get just more complicated, see (35).

Diffusion drives the individual parasite level in both directions, and individuals may be absorbed into U. However, the overall effect of a larger diffusion rate D is to **increase** the mean parasite load.

7. **Expectation and variance.** Size structure models are usually applied to the distribution of body mass in a population. Then x is the mass of an individual and $u(x)$ is the density of the population structured by mass. Such systems can also be interpreted as models for metapopulations. Then x is the population size of a colony and $u(t,x)$ is the density over all occupied colonies (habitats). In the simplest case we have the equation (1). Usually it has been assumed that $g(x)$ is a positive function. Then individuals or colonies never stop growing since death is not included in equation (1).

The solution evolving from an initial condition $u(0,x) = u_0(x)$ can be explicitly represented as in equation (3). To see what happens during a short time interval assume that

$$g(x) = ax + o(x),$$

with $a > 0$, for $x > 0$. Then $G(t,x) \approx e^{at}x$ for small t and thus

$$u(t,x) \approx e^{-at} u_0(e^{-at}x).$$

Mass is conserved since

$$\int_0^\infty e^{-at} u_0(e^{-at}x)dx = \int_0^\infty u(e^{-at}x)d(e^{-at}x) = \int_0^\infty u_0(x)dx.$$

If we have non-negative data with compact support (a hump) u_0 then the hump moves towards larger values of x and gets somewhat wider and flatter. If $g(x)$ is positive for all $x > 0$, then the density is shifting towards larger x all the time.

Now we assume that there is a maximal body size, or a maximal colony size (carrying capacity) in the metapopulation setting. Hence we assume that there is some $K > 0$ such that the function g is positive for $x < K$, but negative for $x > K$. If we follow non-negative solutions of equation (1) with support in $(0, K)$ then we see that the mass is accumulating near $x = K$. There is no equilibrium distribution. The biological interpretation says that for each individual size approaches $x = K$.

Now we add diffusion, for simplicity with a constant diffusion rate,

$$u_t + (g(x)u)_x = Du_{xx}. \tag{45}$$

We look for equilibria. At an equilibrium we have $Du_{xx} - (g(x)u)_x = 0$ and hence $Du_x - g(x)u = aD$ with some constant a. The solution of this equation is

$$u(x) = a \int_0^x e^{\frac{1}{D}\int_s^x g(\tau)d\tau} ds + e^{\frac{1}{D}\int_0^x g(s)ds} u(0).$$

There are two free parameters a and $u(0)$. A no-flux condition at $x = 0$

$$Du_x(0) + g(0)u(0) = 0$$

implies $a = 0$. Then the constant $u(0)$ can be determined from conservation of mass. The normalized equilibrium solution is given by

$$u(x) = \frac{1}{m}e^{\frac{1}{D}\gamma(x)}, \quad m = \int_0^\infty e^{\frac{1}{D}\gamma(x)}dx \tag{46}$$

with

$$\gamma(x) = \int_0^x g(s)ds. \tag{47}$$

The function γ increases in $(0, K)$ and decreases for $x > K$.

What happens for small D? The function γ has a single maximum at $x = K$. If D is small then $1/D$ is large and the function γ/D is very large near $x = K$, compared to points x away from K. The same is true for the function $\exp\{\gamma(x)/D\}$. If we take the normalization factor into account then $u(x)$ is absolutely large near $x = K$ and small everywhere else. Hence the density (46) is concentrated near K. Since we know that $\gamma'(K) = 0$, the behavior of u near K is determined by the value $\gamma(K)$ and by $\gamma''(K)$. So we replace $\gamma(x)$ by

$$\gamma(x) \approx \alpha - \frac{b}{2}(x - K)^2$$

where $\alpha = \gamma(K)$ and $b = -\gamma''(K) = -g'(K)$. Since a factor $\exp\{\alpha/D\}$ drops out, we get the following approximation for $u(x)$,

$$v(x) = \frac{1}{M}e^{-\frac{b}{D}\frac{(x-K)^2}{2}}, \quad M = \int_0^\infty e^{-\frac{b}{D}\frac{(x-K)^2}{2}}dx. \tag{48}$$

The approximation is a censored normal distribution. If D is small then it is essentially a normal distribution with mean $\mu = K$ and variance $\sigma^2 = D/b$. We state this result as a theorem.

Theorem 7.1. *Suppose the differential equation (2) has an exponentially attracting equilibrium K such that $\gamma(K)$ is an absolute maximum of the function γ. Then, for small diffusion rates, the equilibrium distribution is concentrated near K. The distribution is approximately normal with mean and variance*

$$mean = K, \quad variance = \frac{D}{|g'(K)|}. \tag{49}$$

The mean is essentially not affected by diffusion. The variance is influenced by two effects. A small diffusion rate D makes the variance small. If trajectories of the equation (2) approach K rapidly then the variance becomes small. Both findings agree with biological intuition.

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