The mathematical description of the dynamics of structured populations, a brief outline

Odo Diekmann

1 Introduction

The aim of this short note is to explain the main ideas underlying a recent attempt to develop a general mathematical theory concerning models of the dynamics of interacting (physiologically and/or spatially) structured biological populations. For full details we refer to [3, 4, 6, 8].

2 The setting

Let Ω be a set equipped with a countably generated Σ- algebra. A point in Ω corresponds to a possible state of an individual and accordingly we call Ω the i-state space. The population state is a measure on Ω, describing how many individuals there are and how their i-states are distributed. The aim is to specify how the population state evolves in the course of time on the basis of model assumptions concerning the behaviour of individuals. This "behaviour" has several components : movement in Ω, survival, reproduction and interaction. Concerning interaction, we shall restrict ourselves to indirect interaction via environmental quantities, e.g. food and predation pressure.

3 Movement in Ω

As a first modelling ingredient we introduce

$u_t(x, \omega) \simeq$ the probability that an individual that currently has i-state $x \in \Omega$ has time t from now an i-state in $\omega \subset \Omega$

(while assuming that this quantity is bounded and measurable with respect to x and countably additive with respect to ω). We call u_t a positive kernel and note that it is a (possibly defective, because of the possibility of death) transition probability.

Introducing the product

$$(k^2 \times k^1)(x, \omega) := \int_\Omega k^2(\xi, \omega) k^1(x, \mathrm{d}\xi)$$

we have as a natural consistency condition the Chapman-Kolmogorov relation

$$u_{t+s} = u_t \times u_s.$$

Before proceeding to the population level we give two examples of how to construct such a (Green's function, as one may also call it) u_t on the basis of more elementary/basic modeling ingredients.

Example 1 : Let x correspond to the "size" (length or volume or biomass or...) of an individual, which evolves deterministically according to the ode

$$\frac{dx}{dt} = g(x).$$

Let $x(t; x_0)$ denote the unique solution corresponding to the initial condition $x(0; x_0) = x_0$. Assume that individuals of size x experience a force of mortality $\mu(x)$. Define the survival probability $\mathcal{F}(t; x_0)$ as the unique solution of the initial value problem

$$\begin{cases} \frac{d\mathcal{F}}{dt} & = & -\mu(x(\cdot; x_0))\mathcal{F} \\ \\ \mathcal{F}(0; x_0) & = & 1 \end{cases}$$

Finally define

$$u_t(x_0, \omega) = \mathcal{F}(t, x_0)\delta_{x(t; x_0)}(\omega)$$

where, as usual, δ_x denotes the Dirac mass concentrated in x.

Example 2 : Let x correspond to (one-dimensional) spatial position. Assume that individuals diffuse with position-dependent diffusion coefficient $D(x)$. Assume that individuals at position x experience a force of mortality

$\mu(x)$. Let the function $v(t, x; x_0)$ be the unique solution of the pde initial value problem

$$\begin{cases} \frac{\partial v}{\partial t} & = & \frac{\partial}{\partial x}(D(x)\frac{\partial v}{\partial x}) - \mu(x)v \\ v(0, \cdot; x_0) & = & \delta_{x_0}. \end{cases}$$

Then we define

$$u_t(x_0, \omega) = \int_\omega v(t, \xi; x_0)\mathrm{d}\xi.$$

If we consider a population of independent individuals with initial distribution m_0, then its distribution at time t is given by

$$T(t)m_0 = u_t \times m_0$$

(where $(u_t \times m_0)(\omega) = \int_\Omega u_t(\xi, \omega)m_0(\mathrm{d}\xi)$). The Chapman-Kolmogorov relation guarantees that T is a semigroup, i.e.

$$T(t + s) = T(t)T(s), \quad t, s \geq 0.$$

So far, so good, but two essential elements of population biology, viz.

- creation (reproduction)

- dependence (interaction)

are not yet incorporated.

4   Reproduction

As a second modeling ingredient we introduce (adopting a female based bookkeeping system)

> $\Lambda_t(x, \omega) \simeq$ the expected number of daughters with state-at-birth in $\omega \subset \Omega$ of a mother which currently has i-state $x \in \Omega$ in a time interval of length t.

As this is an additive/cumulative quantity, the consistency condition takes a somewhat different form. It reads

$$\Lambda_{t+s} = \Lambda_s + \Lambda_t \times u_s.$$

In addition, since we need to distinguish offspring not only according to the state-at-birth but also according to the time of birth, we need the convolution product

$$(k^2 * k^1)_t = \int_{[0,t)} k^2_{t-\tau} \times k^1_{d\tau}.$$

The point about the convolution product is that it allows us to iterate the reproduction law to obtain the relevant information about grand-daughters, great-grand-daughters etc. Indeed, if we define

$$\Lambda^{1*} = \Lambda$$

$$\Lambda^{(k+1)*} = \Lambda * \Lambda^{k*}, \quad k \geq 1$$

then we can construct the clan kernels

$$\Lambda^c = \sum_{k=1}^{\infty} \Lambda^{k*}$$

$$u^c = u + u * \Lambda^c$$

and therefore the next-population-state operators

$$T(t)m_0 = u^c_t \times m_0.$$

That this construction yields a semigroup of operators is to be expected, but must be verified.

Proposition 1

i) $\Lambda^c_{t+s} = \Lambda^c_s + \Lambda^c_t \times u^c_s$

ii) $u^c_{t+s} = u^c_t \times u^c_s$

iii) $T(t+s) = T(t)T(s)$

The construction of Λ_t from a, say, size-specific reproduction rate $\beta(x)$ (in the context of Example 1 above) is particularly easy if there is only one possible state-at-birth, say x_b. Define $L(t; x_0)$ as the unique solution of the initial value problem

$$\begin{cases} \frac{dL}{dt} = \beta(x(\cdot; x_0))\mathcal{F}(x(\cdot; x_0)) \\ L(0; x_0) = 0 \end{cases}$$

then we put

$$\Lambda_t(x_0, \omega) = L(t; x_0)\delta_{x_b}(\omega).$$

When there are finitely many possible birth states, we get a matrix-vector version of this. The extension to a continuum of possible birth states is straight-forward but, of course, notationally as well as computationally much more involved. In general, the construction of u and Λ from the rates g, μ and β is a preprocessing that corresponds to the integration along characteristics in models formulated as first order pde for population densities, as in [1, 2, 7, 9, 11, 12].

5 Interaction

The formalism developed so far covers linear models, i.e. situations in which individuals behave without affecting each other. It applies whenever the environmental conditions, such as food availability and the probability per unit of time of being caught by a predator, are fixed "in advance", e.g. by an experimenter.

In mathematics one can always pretend, as long as one is explicit about it. So our approach is to first consider the environmental conditions as known/given. In a second step we then determine the environmental conditions from the constructed population development in the course of time. The consistency requirement then takes the form of a fixed point problem, which can be solved. So what we do is to first cut the feedback loop and then restore it.

The kernels u and Λ were provided with an index t corresponding to the time elapsed. We now replace the symbol t by the symbol I, where I denotes the "input" provided on a time interval of length $l(I)$ (corresponding to the t before). So I describes the environmental conditions between now and $l(I)$ from now and, given these, we know how individuals behave in this time interval (in the context of Example 1, the functions g, μ and β now also depend on I). The addition of real numbers (recall $t+s$) is replaced by concatenation (glueing together) of function segments, denoted by the symbol $\odot$:

$$(I_2 \odot I_1)(t) = \begin{cases} I_1(t) & for \quad 0 \le t < l(I_1) \\ I_2(t - l(I_1)) & for \quad l(I_1) \le t < l(I_1) + l(I_2) \end{cases}$$

The Chapman-Kolmogorov relation then takes the form

$$u_{I_2 \odot I_1} = u_{I_2} \times u_{I_1}$$

and the consistency condition for Λ now reads

$$\Lambda_{I_2 \odot I_1} = \Lambda_{I_1} + \Lambda_{I_2} \times u_{I_1}.$$

Starting from u_I and Λ_I one can construct Λ_I^c and u_I^c as before and then define the next population-state operators

$$T_I m_0 = u_I^c \times m_0$$

which form a semigroup

$$T_{I_2 \odot I_1} = T_{I_2} T_{I_1}.$$

The easiest form of feedback is the pure mass action case, in which I itself is a linear functional of the population state (so I is obtained by adding contributions of individuals; more mathematically one should refer to this as a quadratic nonlinearity). If $\gamma(x)$ denotes the i-state specific contribution of an individual to I (so note that γ is yet another modeling ingredient) then the fixed point problem takes the form

$$I(t) = \gamma \times u_{\rho(t)I}^c \times m_0$$

where $\rho(t)I$ denotes the restriction of I to the inverval of length $t < l(I)$ and, in particular, $l(\rho(t)I) = t$.

" **Theorem**" Under appropriate assumptions there is, for given m_0 and small enough $l(I)$, a unique fixed point (depending on m_0 and denoted by I_{m_0}).

A nonlinear semiflow is then obtained by putting

$$S(t, m_0) = T_{\rho(t)I_{m_0}} m_0$$

6   Concluding remarks

Via this construction we have deduced the population development from the rules concerning individual behaviour, together with the initial population state m_0. The presentation above does not touch upon the determination of steady states (and their stability) and, at first, it may seem that the formalism is not very well suited for that. But actually it is! [5], [8].

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