EVOLUTIONARY STABLE STRATEGIES AS ASYMPTOTIC EQUILIBRIA OF MUTATION-SELECTION SYSTEMS

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Many mathematical models in Ecology have the form of a family of differential equations systems like the following

$$(1)_x \begin{cases} u' = A(x,r)u \\ r_i' = F_i(r, L(x)u)r_i, \quad i = 1, \dots, m. \end{cases}$$

Here $u(t)$ belongs to the positive cone of an ordered Banach space X (often $\mathbb{R}^n$, $n \geq 1$) and stands for the population density or the population number of predators of a biological species. x is a real variable playing the role of a parameter in (1) and characterising the individuals of the predator population by some significant feature (as maturation age, see [3], or ability to capture preys, see [1], or time devoted to collecting some specific resource, etc.) capable of affecting the population growth rate for a given resources population (equivalently, in a given environment). $r(t)$ belongs to the positive cone of $\mathbb{R}^m$ and stands for the population number of m different kinds of resources (or preys).

$A(x,r)$ is a linear operator in X which is the infinitesimal generator of a positive semigroup and it is assumed to have a strictly dominant eigenvalue $\lambda(x,r)$ whose corresponding eigenvector $\varphi(x,r)$ is the only positive eigenvector. Moreover $\lambda(x,r)$ is increasing with r_i for all i.

$L(x)$ is a positive continuous linear form in X and, for all i, F_i is a real function of $m+1$ variables decreasing in all its arguments and taking into account the effects of competition and predation on the growth rate of the population of resource i.

A coexistence (i.e. a positive) equilibrium of system (1) is a pair $(c\varphi(x,r), r)$ such that (c,r) is a positive solution of the following system of $m+1$ equations

$$(2)_x \begin{cases} \lambda(x,r) = 0 \\ F_i(r, cL(x)\varphi(x,r)) = 0. \end{cases}$$

In many cases this system has a unique solution due to the monotonicity assumptions and, furthermore, the resulting coexistence equilibrium turns out to be a global attractor for the positive solutions of system $(1)_x$. This is particularly simple when

$$A(x,r) = A(x) - d(r)I,$$

because this form of operator $A(x,r)$ allows to reduce $(1)_x$ to an ordinary differential equations system.

A crucial question in Evolution Theory is what value of the "evolutionary variable" x is chosen in Nature. The answer is given by the so-called Evolutionary Stable (Equilibrium) Strategy (see [2]): a value x^* such that there is a coexistence equilibrium (u^*, r^*) of system $(1)_{x^*}$ and $\lambda(x, r^*) < \lambda(x^*, r^*)$ if $x \neq x^*$.

In [1] it is proposed to substitute system $(1)_x$ where one assumes all predator identical by a system for the density of individuals of characteristic $x \in I$:

$$(3)_\varepsilon \begin{cases} u' = A_\varepsilon(r)u \\ r_i' = F_i(r, \int L(x)u\, dx)r_i. \end{cases}$$

Here $u(t)$ belongs to the positive cone of a Banach space Y of functions on I with values in X and $A_\varepsilon(r)$ is a linear operator in Y which tends in some sense to the multiplication operator $A(x,r)\cdot$ when ε goes to 0. The biological meaning of this is that the growth rate of individuals with characteristic x depends on the whole distribution u when $\varepsilon > 0$ but only on the density $u(x,t)$ when $\varepsilon = 0$. So ε can be viewed as the mutation rate of the characteristic x.

On the other hand, $A_\varepsilon(r)$ is assumed to have also a strictly dominant eigenvalue $\lambda_\varepsilon(r)$ and an associate positive eigenvector $\varphi_\varepsilon(r)$. So the predator population at a coexistence equilibrium is a multiple of $\varphi_\varepsilon(r)$ for some value r. Under reasonable hypotheses one can prove that, for small ε, $\varphi_\varepsilon(r)$ tends to concentrate around the value E.S.(E.)S. x^*. So, for small ε, the E.S.S. turns out to be the asymptotics of an equilibrium (and, even, an attractor) of a system $(3)_\varepsilon$ modelling not only selection (as system $(1)_x$ did) but mutation too.

In [1] an example is considered where X reduces to $\mathbb{R}$, $m = 1$ and the difference operator $A_\varepsilon(r) - A(x,r)\cdot$ consists of a diffusive term $\varepsilon \dfrac{d^2}{dx^2}$.

A more involved example, with infinite dimensional X, is the following model for a young-adult population $(u(t,x,a),\ v(t,x))$ where the evolutionary variable is the maturation age (cf. [3]):

$$\begin{aligned} u_t + u_a + mu &= 0, \quad a \in [0,x], \quad x \in [0,\infty) = I \\ v_t + mv &= u(t,x,x) \\ u(t,x,0) &= \int_0^\infty b(y)\beta_\varepsilon(|x-y|)v(t,y)\, dy. \end{aligned}$$

Here $b(y)$ is the fertility modulus of adults with characteristic y and $\beta_\varepsilon(|x-y|)$ is the probability that an adult y produces an offspring x and tends to a Dirac's delta when ε goes to 0. So, when $\varepsilon = 0$ the third equation reduces to

$$u(t,x,0) = b(x)v(t,x).$$

Referencias

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