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Existence and stability of stationary solutions to spatially extended autocatalytic and hypercyclic systems under global regulation and with nonlinear growth rates

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ABSTRACT

An analytical analysis of spatially extended autocatalytic and hypercyclic systems is presented. It is shown that spatially explicit systems in the form of reaction–diffusion equations with global regulation possess the same major qualitative features as the corresponding local models. In particular, using the introduced notion of the stability in the mean integral sense we prove the competitive exclusion principle for the autocatalytic system and the permanence for the hypercycle system. Existence and stability of stationary solutions are studied. For some parameter values it is proved that stable spatially non-uniform solutions appear.

1. Introduction and background

In 1971 Manfred Eigen published a seminal paper on the evolution of error-prone self-replicating macromolecules [1]. His theory was expanded significantly later on, primarily in the works of Eigen, Schuster and co-workers [2–4]. One of the principal findings was the existence of the *error threshold*, i.e., the critical mutation rate such that the equilibrium population of macromolecules (the *quasispecies* in the terminology of Eigen et al.) cannot provide conditions for evolution if the fidelity of copying falls below this critical level. This critical mutation rate depends on the length of macromolecules and hence puts limits on the amount of information that can be carried by a given macromolecule. To improve fidelity one needs longer sequences (e.g., a more efficient replicase), to have longer sequences one needs better fidelity, hence the chicken–egg problem. An easy and obvious solution to this problem is that the early primordial genomes must have consisted of independently replicating entities, which, generally speaking, would compete with each other (see, e.g., [5] and the references therein).

If we consider a simple mathematical description of independent competing replicators then the usual differential equations for the growth take the following form:

$$\frac{\dot{v}_i}{v_i} = a_i v_i^p - f_1(t), \quad i = 1, \ldots, n, \tag{1.1}$$

where $v_i = v_i(t)$ is the concentration of the ith type of macromolecules, a_i is the rate of replicating, $p > 0$ is the degree of autocatalysis, and $f_1(t)$ is the term which is necessary to keep the total concentration constant, this term depends only on t and not on the index, $f_1(t) = \sum_{i=1}^n a_i v_i^p v_i$ in the present case; easy to see that this is equivalent to the condition $\sum_{i=1}^n v_i = 1$.

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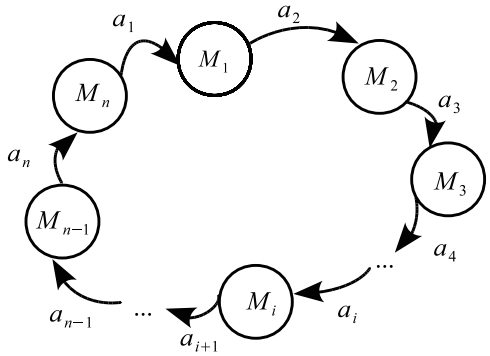

Fig. 1. The hypercycle [4]. Each macromolecule (M_i) helps to replicate another one, M_{i+1}, M_n macromolecule promotes the replication of M_1 closing the loop; a_i, $i = 1, \ldots, n$ denote reaction rates.

In the case if $p \neq 1$ we have a system with nonlinear growth rates, which model different coupling strength of the various components, for the discussion of such growth rates see, e.g., [6,7]. Hereinbelow, we consider mainly $p > 0$ (or even, $p > 1$) but remark that $p = 0$ gives the exponential growth, $p = 1$ gives the standard hyperbolic growth (autocatalysis), and for $p < 0$ the parabolic growth occurs [8]. It is straightforward to show that for $p \geq 0$ only one replicator present at $t \to \infty$, the competition winds up in the *competitive exclusion* of all but one types, i.e., the genome composed of independently replicating entities is not vital.

To resolve this situation Eigen and Schuster [4] suggested a concept of the *hypercycle*, a group of self-replicating macromolecules that catalyze each other in a cyclic manner: the first type helps the second one, the second type helps the third, etc, and the last type helps the first one closing the loop (see Fig. 1). An analogue to system (1.1) can be written in the form

$$\frac{\dot{v}_i}{v_i} = a_i v_{i-1}^p - f_2(t), \quad i = 1, \ldots, n, \tag{1.2}$$

where index 0 coincides with $n, f_2(t) = \sum_{i=1}^n a_i v_{i-1}^p v_i$. For $p = 1$ we obtain the standard hypercycle model [9]. It is known that (1.2) is *permanent*, i.e., all the concentrations are separated from zero, and hence different replicators coexist in this model. More exactly, for short hypercycles, $n = 2, 3, 4$, the internal equilibrium is globally stable, for longer hypercycles, $n > 4$, a globally stable limit cycle appears [10].

The problem with the hypercycle model (1.2) is its vulnerability to the invasion of parasites [11].

We remark that models (1.1) and (1.2) are systems of ordinary differential equations (ODEs), i.e., they are mean field models. As a solution to the parasite invasion problem it was suggested that heterogeneous population structure can strengthen persistence of the system. One of the suggested solutions was spatially explicit models [12–14], see also [15, 16] for reviews of the pertinent work. Two major approaches to spatially explicit models are reaction–diffusion equations and cellular automata models, and they both were considered in the cited works. What was lacking, however, is an analytical treatment of the resulting systems, because in both cases the researchers have resorted to extensive numerical simulations. An only notable exception to our knowledge is [17], where some of the models with explicit space are analyzed analytically. An interest in cluster-like solutions of reaction–diffusion systems resulted in the analysis of spatially explicit hypercycle in infinite space [18,19].

Note that models (1.1) and (1.2) are special cases of the general *replicator equation* [20], for which several approaches are known to incorporate an explicit spatial structure, albeit there is no universally accepted way of incorporating dispersal effects. The solution to the problem with equal diffusion rates is straightforward, in this case we, following ecological approach, can just add the Laplace operator to the right-hand sides of (1.1) or (1.2). This was used, e.g., in the classical paper by Fisher [21] to model the effect of the spatial structure on the invasion properties of an advantageous gene; this approach later was generalized by Hadeler [22]. However, for the primordial world, it would be a too stringent an assumption to have all the diffusion coefficients equal. To overcome this difficulty, Vickers et al. introduced a special form of the population regulation to allow for different diffusion rates [23–25], now in the subject area of evolutionary game dynamics. In these works a nonlinear term is used that provides *local* regulation of the populations under question, although no particular biological mechanism is known that lets individuals adapt their per capita birth and death rates to local circumstances [26]. In our view, it is more natural to assume the *global* regulation of the populations, hence following along the lines of thought that brought to the models (1.1) and (1.2). Mathematically it means that we assume that the total populations satisfy the following condition

$$\sum_{i=1}^n \int_\Omega v_i(t, x)\, \mathrm{d}x = 1,$$

where $x \in \Omega$ is a spatial variable now. This approach was first used in [17]. What is important here is that this approach allows us to obtain some analytical insights into the systems [27].