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Replicator Equations and Space

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Abstract. A reaction–diffusion replicator equation is studied. A novel method to apply the principle of global regulation is used to write down a model with explicit spatial structure. Properties of stationary solutions together with their stability are analyzed analytically, and relationships between stability of the rest points of the non-distributed replicator equation and the distributed system are shown. In particular, we present the conditions on the diffusion coefficients under which the non-distributed replicator equation can be used to describe the number and stability of the stationary solutions to the distributed system. A numerical example is given, which shows that the suggested modeling framework promotes the system's persistence, i.e., a scenario is possible when in the spatially explicit system all the interacting species survive whereas some of them go extinct in the non-distributed one.

Keywords and phrases: replicator equation, reaction-diffusion systems, stability, persistence

Mathematics Subject Classification: 35K57, 35B35, 91A22, 92D25

1. Introduction

The classical replicator equation [15,16] models a wide array of different biological phenomena, including those in theoretical population genetics [15], evolutionary game theory [16,23], or in theories of the origin of life [11]. In its general form, a replicator equation can be written as

$$\dot{w}_i = w_i\big(f_i(\boldsymbol{w}) - f^l(t)\big), \quad i = 1, \dots, n, \tag{1.1}$$

for the vector $\boldsymbol{w} = (w_1, \dots, w_n)$ of system variables. In the following we will speak of $\boldsymbol{w}$ as the vector of concentrations of macromolecules that interact with each other. The interactions are modeled through the rate coefficients (fitnesses) $f_i(\boldsymbol{w})$, which depend in general on the concentrations of other macromolecules. The term $f^l(t)$ is necessary to keep the total concentration $\sum_{i=1}^n w_i$ constant. A particular linear form of the fitnesses is frequently used: $f_i(\boldsymbol{w}) = \sum_{j=1}^n a_{ij} w_j$ for some real matrix $\boldsymbol{A} = (a_{ij})_{n\times n}$, which sometimes called the *interaction matrix*.

Model (1.1) is a system of ordinary differential equations (ODE), which implies that one assumes that there is no spatial structure in the studied system, or, in different words, the reactor that contains the

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macromolecules is so well stirred that any macromolecule has equal chance to interact with any other. For many systems such an assumption is a very crude approximation, therefore it is of significant interest to consider modifications of (1.1) that include explicit spatial structure.

It is well known that the properties of the mean field (ODE) equation often differ in an important way from the properties of the model with spatial structure added (e.g., the whole volume [10] is devoted to this phenomenon). Therefore, the modeler faces two major questions: Firstly, under which circumstances (modeling assumptions) explicit spatial structure changes the model properties such that at least part of the conclusions obtained with the help of the mean-field model are questionable at best, and, secondly, which changes the spatial structure causes to appear.

A standard way to add space in ecological models is to add the Laplace operator to the right hand sides of the system. To be precise, consider a *selection system*

$$\dot{N}_i = N_i g_i(\boldsymbol{N}), \quad i = 1, \dots, n, \tag{1.2}$$

$\boldsymbol{N} = (N_1, \dots, N_n)$, $g_i \colon \mathbf{R}^n_+ \to \mathbf{R}$, which describes, say, interactions and dynamics of n species or macromolecules. Now, to consider the same system without the assumption of the uniform mixing of different species, we replace it with

$$\partial_t N_i = N_i g_i(\boldsymbol{N}) + d_i \Delta N_i, \quad i = 1, \dots, n, \tag{1.3}$$

where now $N_i = N_i(\boldsymbol{x}, t)$, $\boldsymbol{x} \in \Omega \subseteq \mathbf{R}^m$, and d_i are the corresponding diffusion coefficients that describe the macromolecules' motilities. (The precise formulation of the studied systems is given below, together with the initial and boundary conditions.) The same thing cannot be done with system (1.1) because of the fact that there is an additional condition that $\sum_{i=1}^n w_i = \text{const}$ (see also [22] for a thorough discussion). This only works in the case when all the diffusion coefficients d_i are identical (see [14]). Various methods were utilized to overcome this obstacle, see, e.g., [8, 9, 13, 17, 18, 26–29] and references therein.

In particular, if one considers the mean field replicator equation of the form

$$\dot{w}_i = w_i\big((\boldsymbol{A}\boldsymbol{w})_i - \langle \boldsymbol{w}, \boldsymbol{A}\boldsymbol{w}\rangle\big), \quad i = 1, \dots, n, \tag{1.4}$$

where $(\boldsymbol{A}\boldsymbol{w})_i = \sum_{j=1}^n a_{ij} w_j$ and $\langle \cdot, \cdot \rangle$ the standard dot product in $\mathbf{R}^n$, then in [17,18,26–28] the following spatial counterpart for (1.4) was considered:

$$\partial_t N_i = N_i\big((\boldsymbol{A}\boldsymbol{w})_i - \langle \boldsymbol{w}, \boldsymbol{A}\boldsymbol{w}\rangle\big) + d_i \Delta N_i, \quad i = 1, \dots, n, \tag{1.5}$$

which is written for the absolute sizes $\boldsymbol{N}(\boldsymbol{x}, t)$ and not for the frequencies $\boldsymbol{w}(\boldsymbol{x}, t)$. System (1.5) involves the principle of the *local regulation*, which implies that the fitness values at each particular point of the space Ω are determined by the concentrations at this particular point. Arguably this conditions is difficult to justify biologically. In [8,9] another approach was used, when the spatially explicit counterpart of (1.4) is given by

$$\partial_t N_i = N_i\big((\boldsymbol{A}\boldsymbol{w})_i + F(\boldsymbol{N})\big) + d_i \Delta N_i, \quad i = 1, \dots, n, \tag{1.6}$$

where $F(\boldsymbol{N})$ is typically a smooth decreasing function. In (1.6) the population regulation now involves total population sizes $\boldsymbol{N}$, but they also only evaluated at the given point $\boldsymbol{x} \in \Omega$. Moreover, the choice of the function $F(\boldsymbol{N})$ is quite arbitrary. We note that, in addition to the shortcomings mentioned above, systems (1.5) and (1.6) have very different properties (see the references above or [22]).

Our approach to tackle the problem of adding spatial structure to the replicator equation (1.1) or (1.4) is to use the principle of *global regulation* [4–6]. In particular, we start with the original selection system in the form

$$\partial_t N_i = (\boldsymbol{A}\boldsymbol{w})_i N_i + d_i \Delta N_i, \quad i = 1, \dots, n, \tag{1.7}$$

and use the transformation

$$w_i = \frac{N_i}{\sum_j \int_\Omega N_j(\boldsymbol{x}, t)\, \mathrm{d}\boldsymbol{x}},$$

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to end up with the equation of the form

$$\partial_t w_i = w_i\big((\boldsymbol{A}\boldsymbol{w})_i - f_1^{sp}(t)\big) + d_i \Delta w_i, \quad i = 1, \dots, n. \tag{1.8}$$

Here the fitnesses of the subpopulations are regulated by the total sizes, because

$$f_1^{sp}(t) = \int_\Omega \langle \boldsymbol{A}\boldsymbol{w}, \boldsymbol{w}\rangle \, \mathrm{d}\boldsymbol{x}.$$

An extensive analysis of (1.8) is given in [4–6]. One of the main conclusions that we obtained in the cited works is that the behavior of the spatially distributed replicator equation (1.8) with the global regulation is qualitatively similar to the solutions of the mean field model (1.4) in the sense that the interacting populations survive or go extinct in both models for the same parameter values $\boldsymbol{A}$ irrespective of the values of the diffusion coefficients d_i.

A variety of mathematical approaches lead to an informal conclusion that explicit spatial structure mediates coexistence (see, e.g., [10]). Therefore, we would like to offer a modeling approach for the spatially explicit replicator equation that use the principle of the global regulation (which is biologically more plausible than the local regulation) and that at least for some values of the diffusion coefficients and some interaction matrices $\boldsymbol{A}$ guarantees the coexistence of the interacting macromolecules whereas in the non-distributed mean field model some of these macromolecules go extinct. It turns out that the analogy with the diffusion equation in a porous medium [1, 20] allows to achieve this goal. To be specific, instead of (1.7) we consider now

$$\partial_t N_i = (\boldsymbol{A}w)_i N_i + N_i d_i \Delta N_i, \quad i = 1, \dots, n, \tag{1.9}$$

note that N_i are also included in the diffusion coefficients. Using the same normalization, the replicator equation for the frequencies takes the form (all the technical details are presented below)

$$\partial_t w_i = w_i\big((\boldsymbol{A}w)_i - f^{sp}(t) + d_i \Delta w_i\big), \quad i = 1, \dots, n, \tag{1.10}$$

where $f^{sp}(t)$ can be found in Section 2. We call (1.10) the *replicator equation with the global regulation of the second kind*. It turns out that model (1.10) possesses the desired properties. We summarize these properties in non-technical terms:

- For sufficiently large diffusion coefficients d_i the behavior of the solutions to the replicator equation with the global regulation of the second kind (1.10) is qualitatively similar to the mean-field model (1.4) and to the replicator equation with the global regulation of the first kind (1.8) and can be inferred from the analysis of the solutions of the corresponding non-distributed replicator equation (1.4). As expected, in this case the mean-field approximation of a well-stirred reactor works well. We provide the exact statements and proofs in Sections 3 and 4.
- Some of the results concerning the coexistence of the macromolecules for the classical replicator equation (1.4) can be used to obtain sufficient conditions for the coexistence of the macromolecules in the distributed replicator equation (1.10). Section 5 is devoted to the proof of one such result.
- Most importantly, we are able to show (at this stage only numerically) that for sufficiently small diffusion coefficients d_i the properties of the distributed system (1.10) differ significantly from the properties of the non-distributed system (1.4). In particular, the global regulation of the second kind mediates coexistence of different macromolecules, as we show by numerical calculations for a particular replicator system, that is based on in vitro experiments. Whereas the analysis of the local model (1.4) and the distributed replicator equation (1.8) shows that only three out of six interacting macromolecules survive, the numerical solutions to (1.10) demonstrate the coexistence of all six species, in full agreement with the actual experiment, in which coexistence of replicators was studied [25].

Before concluding this section, we would like to note that the equation that we study (system (1.10)) is not a usual reaction-diffusion system, because it includes the functional $f^{sp}(t)$ on the solutions $\boldsymbol{w}$.

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The rest of the paper is organized as follows. In Section 2 we fix the notations and state the mathematical problem, which is in the center of our analysis. For the purpose of comparison we also present the reaction–diffusion replicator systems that we studied in [4–6]. Section 3 is devoted to the analysis of the stationary solutions of the corresponding replicator equations. We find the conditions under which the distributed system behaves similarly to the mean-field model. In Section 4 stability of the stationary solutions is analyzed; again, we are able to prove that some particular knowledge on the stability of the stationary points in the non-distributed case can be used to infer the stability of the stationary state of the distributed system. In a number of situations it is important to guarantee that none of the macromolecules go extinct with time, this condition is formalized mathematically using the notions of *persistence* (e.g., [7]). In Section 5 we obtain a sufficient condition for our system to be persistent. Although a great deal of analysis can be accomplished analytically (Sections 2–5), we also present numerical results to complete the picture. The replicator equation that we study actually possesses the property that even if in the non-distributed system some of the species go extinct, the distributed reaction-diffusion replicator equation supports the existence of all macromolecules; in Section 6 we give an example of such behavior, basing our model on the *in vitro* experiments of RNA self-replicating molecules [25].

2. Problem statement and notations

Let Ω be a bounded domain in $\mathbf{R}^m$ with a piecewise smooth boundary Γ, and m denote the dimension of the problem, we consider only $m = 1, 2$, or 3. Without loss of generality we assume that $|\Omega| = 1$, i.e., the volume of Ω is equal to 1. Denote $N_k(\boldsymbol{x}, t)$ the number of macromolecules of the k-th type, $k = 1, \ldots, n$, per volume unit at the time moment t at the point $\boldsymbol{x} \in \Omega \subset \mathbf{R}^m$. We postulate that the relative rate of change of $N_k(\boldsymbol{x}, t)$ at the point $\boldsymbol{x} \in \Omega$ is governed by the following law

$$\frac{\partial_t N_k(\boldsymbol{x}, t)}{N_k(\boldsymbol{x}, t)} = \big(\boldsymbol{A}\boldsymbol{N}(\boldsymbol{x}, t)\big)_k + d_k \Delta N_k(\boldsymbol{x}, t), \quad k = 1, \ldots, n, \tag{2.1}$$

where $\partial_t N_k(\boldsymbol{x}, t) = \frac{\partial N_k}{\partial t}(\boldsymbol{x}, t)$, $\boldsymbol{N}(\boldsymbol{x}, t) = (N_1(\boldsymbol{x}, t), \ldots, N_n(\boldsymbol{x}, t))$, $\boldsymbol{A} = (a_{ks})_{n\times n}$ is an $n \times n$ real matrix,

$$\big(\boldsymbol{A}\boldsymbol{N}(\boldsymbol{x}, t)\big)_k = \sum_{s=1}^{n} a_{ks} N_s(\boldsymbol{x}, t),$$

Δ is the Laplace operator, in Cartesian coordinates $\Delta = \sum_{i=1}^{m} \frac{\partial^2}{\partial x_i^2}$, $m = 1, 2, 3$, $d_k > 0$ are the numbers that characterize the influence of the uniform diffusion on the rate of change of the densities $N_k(\boldsymbol{x}, t)$, $k = 1, \ldots, n$.

A possible interpretation of (2.1) is that we consider a porous medium diffusion equation

$$\phi_k \partial_t N_k = f_k(\boldsymbol{N}) + \Delta N_k, \quad k = 1, \ldots, n,$$

for which the porosity ϕ_k depends on the local concentrations $N_k(\boldsymbol{x}, t)$: $\phi_k(N_k(\boldsymbol{x}, t)) = N_k^{-1}(\boldsymbol{x}, t)$, which means that inverse in the number of particles reduces the space available (for the diffusion equation in a porous medium see, e.g., [1, 20]).

The initial conditions are

$$N_k(\boldsymbol{x}, t) = \Psi_k(\boldsymbol{x}), \quad k = 1, \ldots, n, \tag{2.2}$$

and the boundary conditions are

$$\left.\frac{\partial N_k(\boldsymbol{x}, t)}{\partial \nu}\right|_{\boldsymbol{x}\in\Gamma} = 0, \quad k = 1, \ldots, n, \tag{2.3}$$

where ν is the outward normal to the boundary Γ of Ω. Condition (2.3) describes the zero flux of the macromolecules through boundary Γ.

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System (2.1)–(2.3) defines a *selection system* [19]. It is usually more convenient to replace such system with the corresponding *replicator equation*, which describes the change of frequencies (see, e.g., [22]).

Let

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

and assume for the following that $\Sigma(t) > 0$ for any $t \geq 0$. Then the corresponding frequencies of macromolecules are defined as

$$v_k(\boldsymbol{x}, t) = \frac{N_k(\boldsymbol{x}, t)}{\Sigma(t)}, \quad k = 1, \ldots, n.$$

By construction we have

$$\sum_{k=1}^{n} \int_{\Omega} v_k(\boldsymbol{x}, t)\, \mathrm{d}\boldsymbol{x} = 1. \tag{2.4}$$

Direct calculations lead to

$$\partial_t v_k(\boldsymbol{x}, t) = \Sigma(t) v_k(\boldsymbol{x}, t) \Big(\big(\boldsymbol{A}\boldsymbol{v}(\boldsymbol{x}, t)\big)_k - f^{sp}(t) + d_k \Delta v_k(\boldsymbol{x}, t) \Big), \quad k = 1, \ldots, n,$$

where

$$f^{sp}(t) = \int_{\Omega} \Big(\langle \boldsymbol{A}\boldsymbol{v}(\boldsymbol{x}, t), \boldsymbol{v}(\boldsymbol{x}, t) \rangle + \sum_{k=1}^{n} d_k v_k(\boldsymbol{x}, t) \Delta v_k(\boldsymbol{x}, t) \Big)\, \mathrm{d}\boldsymbol{x}.$$

Hereinafter $\langle \cdot, \cdot \rangle$ denotes the standard inner product in $\mathbf{R}^n$, $\boldsymbol{v}(\boldsymbol{x}, t) = (v_1(\boldsymbol{x}, t), \ldots, v_n(\boldsymbol{x}, t))$. Note that from (2.3) it follows that for the frequencies $v_k(\boldsymbol{x}, t)$ the boundary conditions

$$\left. \frac{\partial v_k(\boldsymbol{x}, t)}{\partial \nu} \right|_{\boldsymbol{x} \in \Gamma} = 0, \quad k = 1, \ldots, n \tag{2.5}$$

hold. Therefore, using Green's identity, the expression for $f^{sp}(t)$ can be rewritten as

$$f^{sp}(t) = \int_{\Omega} \Big(\langle \boldsymbol{A}\boldsymbol{v}(\boldsymbol{x}, t), \boldsymbol{v}(\boldsymbol{x}, t) \rangle - \sum_{k=1}^{n} d_k \sum_{i=1}^{m} \left[\frac{\partial v_k(\boldsymbol{x}, t)}{\partial x_i} \right]^2 \Big)\, \mathrm{d}\boldsymbol{x}. \tag{2.6}$$

The last term in (2.6) can be rewritten in the form $\sum_{k=1}^{n} d_k \langle \nabla v_k, \nabla v_k \rangle = \sum_{k=1}^{n} d_k \|\nabla v_k\|^2$. Note that expression (2.6) for any $t \geq 0$ is a functional defined on the set of vector-functions $\boldsymbol{v}(\boldsymbol{x}, t)$.

Letting $t = \int_0^{\tau} \Sigma(\varsigma)\, \mathrm{d}\varsigma$, we finally obtain the system

$$\partial_\tau v_k(\boldsymbol{x}, \tau) = v_k(\boldsymbol{x}, \tau) \Big(\big(\boldsymbol{A}\boldsymbol{v}(\boldsymbol{x}, \tau)\big)_k - f^{sp}(\tau) + d_k \Delta v_k(\boldsymbol{x}, \tau) \Big), \quad k = 1, \ldots, n, \tag{2.7}$$

with the initial conditions

$$v_k(\boldsymbol{x}, 0) = \varphi_k(\boldsymbol{x}) = \frac{\Psi_k(\boldsymbol{x})}{\sum_j \int_{\Omega} \Psi_k(\boldsymbol{x})\, \mathrm{d}\boldsymbol{x}}, \quad k = 1, \ldots, n, \tag{2.8}$$

which follow from (2.2), and boundary conditions (2.5).

Note that from (2.7) and equality (2.6), taking into account (2.5), we have that

$$\frac{\partial}{\partial \tau} \Big(\sum_{k=1}^{n} \int_{\Omega} v_k(\boldsymbol{x}, \tau)\, \mathrm{d}\boldsymbol{x} \Big) = 0,$$

which corresponds to (2.4).

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In the following we will call the functional $f^{sp}(t)$ *the mean fitness* of the population of macromolecules, whereas the quantity $\big(\boldsymbol{A}\boldsymbol{v}(\boldsymbol{x},t)\big)_k$ will be referred to as the *fitness* of the k-th macromolecule at the point $\boldsymbol{x}\in\Omega$ at the time moment τ. From now on we will also use the variable t instead of τ, keeping in mind that this is a rescaled time.

System (2.4)–(2.8) will be called *the reaction–diffusion replicator equation with the global regulation of the second kind* as opposed to the reaction–diffusion replicator equation with the global regulation of the first kind (see [22] for a concise review on the reaction–diffusion replicator systems and [2–6] for an in-depth analysis of such systems). We recall that in the cited papers dynamics and the limit behavior of the replicator systems of the form

$$\partial_t v_k(\boldsymbol{x},t)=v_k(\boldsymbol{x},t)\Big(\big(\boldsymbol{A}\boldsymbol{v}(\boldsymbol{x},t)\big)_k-f_1^{sp}(t)\Big)+d_k\Delta v_k(\boldsymbol{x},t),\quad k=1,\dots,n, \tag{2.9}$$

was studied. In (2.9) the mean fitness $f_1^{sp}(t)$ is given by

$$f_1^{sp}(t)=\int_\Omega\langle\boldsymbol{A}\boldsymbol{v}(\boldsymbol{x},t),\boldsymbol{v}(\boldsymbol{x},t)\rangle\,\mathrm{d}\boldsymbol{x}, \tag{2.10}$$

and $v_k(\boldsymbol{x},t)$ are nonnegative functions satisfying (2.4), (2.5), and (2.8).

Therefore, systems (2.4)–(2.8) and (2.9)–(2.10) differ both by the form of the equations and by the expressions for the mean population fitness, coinciding in the limit $d_k\to 0$. The mean fitness $f_1^{sp}(t)$ of the system (2.9), (2.10) does not depend on the spatially non-uniform distribution and coincides in the form with the usual mean fitness for the non-distributed replicator equation [15,16]. At the same time, the mean fitness $f^{sp}(t)$ of (2.4)–(2.8) includes the dependence on the square of the expression that characterizes the rate of change of the form of the spatially non-uniform distribution of the densities. This is an important feature of the reaction–diffusion replicator equation with the global regulation of the second kind. Eventually, both of the systems (2.4)–(2.8) and (2.9)–(2.10) represent possible generalizations of the classical replicator equation (1.1) for the case of explicit spatial structure under different principles of global regulation (see Section 1 for more details).

In the following we assume that the functions $v_k(\boldsymbol{x},t)$, $\boldsymbol{x}\in\Omega$, $t\ge 0$, $k=1,\dots,n$ are differentiable with respect to t, and, together with their derivatives with respect to t, belong to the Sobolev space $W^{1,2}(\Omega)$ if $m=1$, or to $W^{2,2}(\Omega)$ if $m=2,3$, as functions of the variable $\boldsymbol{x}\in\Omega$ for each fixed t. Here $W^{r,2}(\Omega)$ are the usual Sobolev spaces such that their elements belong to $L^2(\Omega)$ together with all the (weak) derivatives up to the order r. We note that the embedding theorems imply that the elements of $W^{r,2}(\Omega)$, $r=1,2$ coincide with continuous functions on Ω almost everywhere (e.g., [12]).

Denote $\Omega_t=\Omega\times[0,\infty)$ and consider the space of functions $B(\Omega_t)$ with the norm

$$\|y\|_{B(\Omega_t)}=\max_{t\ge 0}\big\{\|y(\boldsymbol{x},t)\|_{W^{r,2}}+\|\partial_t y(\boldsymbol{x},t)\|_{W^{r,2}}\big\},\quad r=1,2.$$

Let $S_n(\Omega_t)$ denote the set of functions from $B(\Omega_t)$ for which (2.4) holds. The set $S_n(\Omega_t)$ is *an integral simplex* in the space $B(\Omega_t)$. Together with $S_n(\Omega_t)$ also consider the set $S_n(\Omega)$ of the vector-functions $\boldsymbol{u}(\boldsymbol{x})=(u_1(\boldsymbol{x}),\dots,u_n(\boldsymbol{x}))$ such that $u_k(\boldsymbol{x})\in W^{r,2}(\Omega)$ $(r=1,2)$ for which

$$\sum_{k=1}^n\int_\Omega u_k(\boldsymbol{x})\,\mathrm{d}\boldsymbol{x}=1 \tag{2.11}$$

holds. The set $S_n(\Omega)$ is *an integral simplex* in the space $W^{r,2}(\Omega)$, $(r=1,2)$. We consider *weak* solutions to the system (2.4)–(2.8).

Together with the problem (2.4)–(2.8) consider the classical replicator equation (e.g., [15])

$$\dot w_k(t)=w_k(t)\Big(\big(\boldsymbol{A}\boldsymbol{w}(t)\big)_k-f^l(t)\Big),\quad k=1,\dots,n, \tag{2.12}$$

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where $f^l(t) = \langle \boldsymbol{A}\boldsymbol{w}(t), \boldsymbol{w}(t)\rangle$. The system (2.12) is defined on the simplex S_n of smooth nonnegative functions $\boldsymbol{w}(t) = (w_1(t), \dots, w_n(t))$ such that

$$\sum_{k=1}^{n} w_k(t) = 1$$

for any t.

We will also need the definitions of the boundary and interior sets of the (integral) simplex $S_n(\Omega_t)$ (or $S_n(\Omega)$, or S_n).

Definition 2.1. The boundary set $\operatorname{bd} S_n(\Omega_t)$ of $S_n(\Omega_t)$ is the set of vector-functions $\boldsymbol{v}(\boldsymbol{x}, t) \in S_n(\Omega_t)$ such that for some indexes $k \in K$ in the subset $K \subset \{1, \dots, n\}$ one has

$$\overline{v}_k(t) = 0, \quad k \in K,\ t \geq 0,$$

where

$$\overline{v}_k(t) = \int_\Omega v_k(\boldsymbol{x}, t)\, \mathrm{d}\boldsymbol{x}.$$

The interior set $\operatorname{int} S_n(\Omega_t)$ is the set of functions $\boldsymbol{v}(\boldsymbol{x}, t) \in S_n(\Omega_t)$ such that

$$\overline{v}_k(t) > 0, \quad k = 1, \dots, n,$$

for any $t \geq 0$.

Note that due to (2.4) we have for the elements of $\operatorname{bd} S_n(\Omega_t)$

$$\sum_{k \notin K} \int_\Omega v_k(\boldsymbol{x}, t)\, \mathrm{d}\boldsymbol{x} = 1.$$

Analogously, for the system (2.12) and the standard simplex S_n its boundary and interior sets are defined, respectively, as the set which has at least one coordinate $w_k(t) = 0$ and the set for which all the coordinates $w_k(t) > 0$ for $k = 1, \dots, n$. Note that these sets are invariant for (2.12).

Remark 2.2. Since $v_k(\boldsymbol{x}, t) \in W^{r,2}(\Omega)$, $r = 1, 2$ for any fixed $t \geq 0$, this implies that $v_k(\boldsymbol{x}, t)$ coincide with continuous functions almost everywhere. Therefore, $\overline{v}_k(t) = 0$ implies that $v_k(\boldsymbol{x}, t) = 0$ almost everywhere in Ω.

Remark 2.3. For any element $\boldsymbol{v}(\boldsymbol{x}, t) \in \operatorname{bd} S_n(\Omega_t)$ an element $\boldsymbol{w}(t) \in \operatorname{bd} S_n$ can be identified. Indeed, we can always put $\boldsymbol{w}(t) = \overline{\boldsymbol{v}}(t)$.

3. Stationary solutions to the distributed replicator equation

The stationary solutions to the problem (2.4)–(2.8) are determined by the following time independent system of equations

$$u_k(\boldsymbol{x})\Big(\big(\boldsymbol{A}\boldsymbol{u}(\boldsymbol{x})\big)_k - \overline{f}^{sp} + d_k \Delta u_k(\boldsymbol{x})\Big) = 0, \quad k = 1, \dots, n, \tag{3.1}$$

with the boundary conditions

$$\left.\frac{\partial u_k(\boldsymbol{x})}{\partial \nu}\right|_{\boldsymbol{x} \in \Gamma} = 0, \quad k = 1, \dots, n, \tag{3.2}$$

and

$$\overline{f}^{sp} = \int_\Omega \big(\langle \boldsymbol{A}\boldsymbol{u}(\boldsymbol{x}), \boldsymbol{u}(\boldsymbol{x})\rangle - \sum_{k=1}^{n} d_k \|\nabla u_k(\boldsymbol{x})\|^2\big)\, \mathrm{d}\boldsymbol{x}. \tag{3.3}$$

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Solutions to (3.1)–(3.3) will be sought both in the set $\operatorname{int} S_n(\Omega)$ and in the set $\operatorname{bd} S_n(\Omega)$. Together with the solutions to (3.1)–(3.3), consider the stationary points of (2.12), which are given as the solutions to

$$w_k\big((\boldsymbol{A}\boldsymbol{w})_k - \langle \boldsymbol{A}\boldsymbol{w}, \boldsymbol{w}\rangle\big) = 0, \quad \boldsymbol{w} \in S_n, \quad k = 1, \ldots, n. \tag{3.4}$$

Consider an auxiliary eigenvalue problem for the eigenfunctions $\psi(\boldsymbol{x})$

$$\Delta\psi(\boldsymbol{x}) + \lambda\psi(\boldsymbol{x}) = 0, \quad \boldsymbol{x} \in \Omega, \quad \partial_\nu\psi|_{\boldsymbol{x}\in\Gamma} = 0. \tag{3.5}$$

The eigenfunction system of (3.5) is given by $\psi_0(\boldsymbol{x}) = 1$, $\{\psi_i(\boldsymbol{x})\}_{i=1}^{\infty}$ and forms a complete system in the Sobolev space $W^{r,2}(\Omega)$, $r = 1, 2$ (e.g., [21]), additionally

$$\int_\Omega \psi_i(\boldsymbol{x})\psi_j(\boldsymbol{x})\,\mathrm{d}\boldsymbol{x} = \delta_{ij}, \tag{3.6}$$

where δ_{ij} is the Kronecker symbol. The corresponding eigenvalues satisfy the condition

$$0 = \lambda_0 < \lambda_1 \le \lambda_2 \le \ldots \le \lambda_i \le \ldots, \qquad \lim_{i\to\infty} \lambda_i = +\infty.$$

It it convenient to introduce the following definition.

Definition 3.1. We shall call the diffusion coefficient d_k of the system (3.1) μ-resonant if there exists an eigenvalue λ_{s_k} of (3.5) such that

$$d_k = \frac{\mu}{\lambda_{s_k}}. \tag{3.7}$$

By definition μ has to a be a positive constant. From the definition it follows that if

$$d_{\min} > \frac{\mu}{\lambda_1}, \quad d_{\min} = \min\{d_1, \ldots, d_n\} \tag{3.8}$$

for a given μ, then all the diffusion coefficients are not μ-resonant.

Theorem 3.2. *Let $\boldsymbol{A}$ have at least one real eigenvalue and let μ be the maximal eigenvalue of $\boldsymbol{A}$. Assume also that system* (3.4) *has an isolated solution $\boldsymbol{w} \in \operatorname{int} S_n$. If condition* (3.8) *holds then all the stationary solutions $\boldsymbol{u}(\boldsymbol{x}) \in \operatorname{int} S_n(\Omega)$ of the distributed system* (2.4)–(2.8) *are spatially uniform and coincide with the interior rest point $\boldsymbol{w} \in \operatorname{int} S_n$ of* (2.12).

Proof. Let $\boldsymbol{u}(\boldsymbol{x}) \in \operatorname{int} S_n(\Omega)$ be a solution to (3.1)–(3.3). Then

$$\big(\boldsymbol{A}\boldsymbol{u}(\boldsymbol{x})\big)_k - \overline{f}^{sp} + d_k\Delta u_k(\boldsymbol{x}) = 0, \quad \partial_\nu u_k = 0, \quad k = 1, \ldots, n. \tag{3.9}$$

Let us look for a solution to (3.9) in the form of a series with the basis $\psi_0(\boldsymbol{x}) = 1$, $\{\psi_i(\boldsymbol{x})\}_{i=1}^{\infty}$ of solutions to (3.5):

$$u_k(\boldsymbol{x}) = \overline{u}_k + U_k(\boldsymbol{x}), \quad U_k(\boldsymbol{x}) = \sum_{s=1}^{\infty} c_s^k\psi_s(\boldsymbol{x}), \tag{3.10}$$

where

$$\overline{u}_k = \int_\Omega \psi_0(\boldsymbol{x})u_k(\boldsymbol{x})\,\mathrm{d}\boldsymbol{x} = \int_\Omega u_k(\boldsymbol{x})\,\mathrm{d}\boldsymbol{x}.$$

Putting (3.10) into (3.9), integrating through Ω, and taking into account (3.6), we find

$$(\boldsymbol{A}\overline{\boldsymbol{u}})_1 = \ldots = (\boldsymbol{A}\overline{\boldsymbol{u}})_n = \overline{f}^{sp}. \tag{3.11}$$

Then from (3.10) and (3.9) it follows that for each k

$$\big(\boldsymbol{A}\boldsymbol{U}(\boldsymbol{x})\big)_k = -d_k\Delta U_k(\boldsymbol{x}), \quad \boldsymbol{U}(\boldsymbol{x}) = \big(U_1(\boldsymbol{x}), \ldots, U_n(\boldsymbol{x})\big), \tag{3.12}$$

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which implies

$$d_k \sum_{s=1}^{\infty} c_s^k \lambda_s \psi_s(\boldsymbol{x}) = \sum_{j=1}^{n} a_{kj} \sum_{s=1}^{\infty} c_s^j \psi_s(\boldsymbol{x}).$$

Taking the inner product of the last equality with $\psi_s(\boldsymbol{x})$ in $L^2(\Omega)$ and using (3.6), we obtain that the coefficients c_s^k have to be solutions of the following linear systems

$$(\boldsymbol{A} - d_k \lambda_s \boldsymbol{I})\boldsymbol{c}^s = 0, \quad \boldsymbol{c}^s = (c_s^1, \dots, c_s^n)^\top, \quad s = 1, 2, \dots \tag{3.13}$$

where $\boldsymbol{I}$ is the identity matrix. If the assumptions of the theorem hold, then systems (3.13) have only trivial solutions $\boldsymbol{c}^s = 0$, which implies that $u_k(\boldsymbol{x}) = \overline{u}_k$ for all k and $\overline{f}^{sp} = \langle \boldsymbol{A}\overline{\boldsymbol{u}}, \overline{\boldsymbol{u}} \rangle$, therefore the solution to (3.11) coincides with the solution to (3.4). □

The results of Theorem 3.2 can be generalized for the case when solutions to (3.1)–(3.3) are taken from $\operatorname{bd} S_n(\Omega)$. Let $\boldsymbol{u}(\boldsymbol{x}) \in \operatorname{bd} S_n(\Omega)$. Then there exists set $K \subset \{1, \dots, n\}$ from Definition 2.1. Denote $\boldsymbol{A}_K$ the matrix which is obtained from $\boldsymbol{A}$ by deleting the rows and columns with indexes from K.

Corollary 3.3. *Let $\boldsymbol{A}_K$ have at least one real eigenvalue and let μ be the maximal eigenvalue of $\boldsymbol{A}_K$. Also assume that there exists an isolated solution $\boldsymbol{w} \in \operatorname{bd} S_n$ to* (3.4) *with $\boldsymbol{A} = \boldsymbol{A}_K$. If condition* (3.8) *on the set of $k \notin K$ holds, then all the solutions $\boldsymbol{u}(\boldsymbol{x}) \in \operatorname{bd} S_n(\Omega)$ are spatially uniform and coincide with the solutions $\boldsymbol{w} \in \operatorname{bd} S_n$ to* (2.12).

The proof follows the steps of the proof of Theorem 3.2.

Corollary 3.4. *Let $\boldsymbol{A}$ have at least one real eigenvalue and let μ be the maximal eigenvalue of $\boldsymbol{A}$. Assume also that system* (3.4) *has an isolated solution $\boldsymbol{w} \in \operatorname{int} S_n$. If problem* (3.1)–(3.3) *possesses μ-resonant diffusion coefficients, then it has infinitely many spatially nonuniform solutions, whose mean integral values coincide with the solution to* (3.4).

Proof. In this case systems (3.13) have infinitely many solutions. If each of equalities in (3.12) is multiplied by $U_k(\boldsymbol{x})$ and integrated over Ω, then we obtain

$$\int_\Omega \langle \boldsymbol{A}\boldsymbol{U}(\boldsymbol{x}), \boldsymbol{U}(\boldsymbol{x}) \rangle \, \mathrm{d}\boldsymbol{x} = \sum_{k=1}^{n} d_k \int_\Omega \langle \nabla U_k(\boldsymbol{x}), \nabla U_k(\boldsymbol{x}) \rangle \, \mathrm{d}\boldsymbol{x}. \tag{3.14}$$

From the representation of $\overline{f}^{sp}$ in (3.3) and series (3.10) we have

$$\langle \boldsymbol{A}\overline{\boldsymbol{u}}, \overline{\boldsymbol{u}} \rangle = \overline{f}^{sp}. \tag{3.15}$$

The equality (3.15) together with (3.11) imply that $\overline{\boldsymbol{u}} = \boldsymbol{w}$, where $\boldsymbol{w}$ solves (3.4). □

Example 3.5. Consider stationary solutions when $\boldsymbol{A}$ is a circulant matrix:

$$\boldsymbol{A} = \begin{bmatrix} a_1 & a_2 & \dots & a_{n-1} & a_n \\ a_n & a_1 & \dots & a_{n-2} & a_{n-1} \\ \dots & & & & \\ a_2 & a_3 & \dots & a_n & a_1 \end{bmatrix}.$$

If $\mu = \sum_{i=1}^{n} a_i > 0$ then, according to Corollary 3.4, there are infinitely many spatially nonhomogeneous solutions to (3.1)–(3.3) if, e.g.,

$$d_{\max} = \frac{\mu}{\lambda_1}, \quad d_{\max} = \max\{d_1, \dots, d_n\}.$$

If $\mu < 0$, then the number of stationary solutions is finite and they coincide with the solutions to (3.4) corresponding to the replicator equation (2.12).

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Before closing this section, we would like to stress an interesting feature of the problem (3.1)–(3.3): It is possible to find such $\boldsymbol{u}(\boldsymbol{x}) \in \operatorname{int} S_n(\Omega)$ satisfying the boundary condition (3.2), that on some domain $\Omega_k \subset \Omega$ the function $u_k(\boldsymbol{x}) \equiv 0$ when $\boldsymbol{x} \in \Omega_k$, whereas on $\Omega \setminus \Omega_k$ $u_k(\boldsymbol{x})$ satisfies (3.1) and (3.3). We illustrate this assertion with an example.

Example 3.6. Consider an autocatalytic system on $\Omega = (0,1)$. This means that the matrix $\boldsymbol{A}$ is diagonal, $\boldsymbol{A} = \operatorname{diag}(a_1, \dots, a_n)$, and the stationary solutions solve

$$u_k(x)\Big(d_k \frac{d^2 u_k}{dx^2}(x) + a_k u_k(x) - \overline{f}^{sp}\Big) = 0, \quad a_k > 0, \quad k = 1, \dots, n,$$
$$u_k'(0) = u_k'(1) = 0, \quad \overline{f}^{sp} = \sum_{k=1}^{n} \int_0^1 \Big(a_k u_k^2(x) - d_k\big(u_k'(x)\big)^2\Big)\,\mathrm{d}x.$$

Assume that

$$\sqrt{\frac{a_1}{d_1}} = m\pi$$

for some positive integer $m \geq 1$, whereas for the rest of the parameters $a_k/d_k < \pi$ for $k = 2, \dots, n$. Then solutions have the form

$$u_1(x) = c_1 \cos m\pi x + \frac{\overline{f}^{sp}}{a_1}, \quad u_k(x) = \frac{\overline{f}^{sp}}{a_k}, \quad k = 2, \dots, n,$$

and since $\boldsymbol{u}(x) \in S_n(0,1)$ then the following condition

$$\overline{f}^{sp} = \frac{1}{\sum_{k=1}^{n} a_k^{-1}}$$

should hold. This can be checked directly, since

$$\overline{f}^{sp} = \int_0^1 \Big(a_1 u_1^2(x) - d_1\big(u_1'(x)\big)^2 + \sum_{k=2}^{n} a_k u_k^2(x)\Big)\,\mathrm{d}x = \big(\overline{f}^{sp}\big)^2 \sum_{k=1}^{n} \frac{1}{a_k},$$

which yields the required equality.

To guarantee that $u_1(x)$ is nonnegative, it is enough to require $|c_1| \leq \overline{f}^{sp}/a_1$. Since c_1 is arbitrary, we found infinitely many stationary solutions (cf. Corollary 3.4). Apart from this set, as it can be directly verified, the following choices for $u_1(x)$ are also solutions:

$$u_1(x) = \begin{cases} \frac{\overline{f}^{sp}}{a_1}(1 + \cos m\pi x), & 0 < x < \frac{1}{m} \\ 0, & \frac{1}{m} \leq x < 1 \end{cases}$$
$$u_1(x) = \begin{cases} 0, & 0 < x \leq \frac{m-1}{m} \\ \frac{\overline{f}^{sp}}{a_1}(1 + (-1)^m \cos m\pi x), & \frac{m-1}{m} < x < 1 \end{cases}$$
$$u_1(x) = \begin{cases} 0, & 0 < x \leq \frac{m-2}{2m} \\ \frac{\overline{f}^{sp}}{a_1}(1 + (-1)^m \cos m\pi x), & \frac{m-2}{2m} < x < \frac{m+2}{2m} \\ 0, & \frac{m+2}{2m} \leq x < 1 \end{cases}$$

The list of examples can be continued. Moreover, similar examples can be constructed in case when Ω is a rectangular area in $\mathbf{R}^2$ or in $\mathbf{R}^3$. The key condition for such solutions to appear is the existence of μ-resonant diffusion coefficients.

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4. Stability of the stationary solutions

In the previous section we identified the conditions on the diffusion coefficients under which the stationary points of the distributed replicator equations are exactly the rest points of the mean field replicator equation. In this section we show that the stability properties of these stationary solutions coincide. In particular, the following theorem holds.

Theorem 4.1. *Let μ be the maximal real part of the eigenvalues of matrix $\boldsymbol{A}$. Assume also that system* (3.4) *has an isolated solution $\boldsymbol{w} \in \operatorname{int} S_n$. If condition* (3.8) *holds then the asymptotic stability (or instability) of the interior rest point $\boldsymbol{w} \in \operatorname{int} S_n$ of the replicator equation* (2.12) *implies asymptotic stability (or instability) of the interior stationary solution to* (2.4)–(2.8).

Proof. Theorem 3.2 yields that the interior stationary point coincides with the interior stationary point of (2.12). Fix an $\varepsilon > 0$ and look for a solution to (2.4)–(2.8) in the form

$$v_k(\boldsymbol{x}, t) = w_k + c_k^0(t) + \sum_{s=1}^{\infty} c_s^k \psi_s(\boldsymbol{x}), \quad k = 1, \ldots, n, \tag{4.1}$$

where $\psi_k(\boldsymbol{x})$ are the eigenfunctions of the problem (3.5), assuming that the initial conditions $v_k(\boldsymbol{x}, 0) = \varphi_k(\boldsymbol{x})$ satisfy

$$\|\varphi_k(\boldsymbol{x}) - w_k\|_{L^2(\Omega)} < \delta, \quad k = 1, \ldots, n. \tag{4.2}$$

Plugging (4.1) into (2.7), integrating over Ω and keeping only linear terms with respect to $c_k^0(t)$, we obtain the following system of linear equations:

$$\frac{dc_k^0(t)}{dt} = w_k \left[\left(\boldsymbol{A}\boldsymbol{c}^0\right)_k - \langle \boldsymbol{A}^\top \boldsymbol{w}, \boldsymbol{c}^0(t) \rangle - \langle \boldsymbol{A}\boldsymbol{w}, \boldsymbol{c}^0(t) \rangle \right] + c_k^0 \left[\left(\boldsymbol{A}\boldsymbol{w}\right)_k - \langle \boldsymbol{A}\boldsymbol{w}, \boldsymbol{w} \rangle \right], \tag{4.3}$$

where $k = 1, \ldots, n$. By virtue of

$$1 = \sum_{k=1}^{n} \int_{\Omega} v_k(\boldsymbol{x}, t)\, \mathrm{d}\boldsymbol{x} = \sum_{k=1}^{n} w_k + \sum_{k=1}^{n} c_k^0(t)$$

and

$$\sum_{k=1}^{n} w_k = 1,$$

we have

$$\sum_{k=1}^{n} c_k^0(t) = 0. \tag{4.4}$$

Therefore, from (3.4) it follows that

$$\langle \boldsymbol{A}\boldsymbol{w}, \boldsymbol{c}^0(t) \rangle = \sum_{k=1}^{n} c_k^0(t) \left(\boldsymbol{A}\boldsymbol{w}\right)_k = f^l \sum_{k=1}^{n} c_k^0(t) = 0,$$

and

$$\langle \boldsymbol{A}\boldsymbol{w}, \boldsymbol{w} \rangle = \left(\boldsymbol{A}\boldsymbol{w}\right)_k, \quad k = 1, \ldots, n.$$

System (4.3) now reads

$$\frac{dc_k^0(t)}{dt} = w_k \left[\left(\boldsymbol{A}\boldsymbol{c}^0\right)_k - \langle \boldsymbol{A}^\top \boldsymbol{w}, \boldsymbol{c}^0(t) \rangle \right], \quad k = 1, \ldots, n. \tag{4.5}$$

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The Jacobi matrix of system (4.5) coincides with the Jacobi matrix of (2.12) evaluated at the interior stationary point $\boldsymbol{w} \in \operatorname{int} S_n$ given by (3.4). Therefore, if $\boldsymbol{w}$ is asymptotically stable (unstable), then the trivial solution to (4.5) is also asymptotically stable (unstable).

Now we plug (4.1) into (2.7), multiply consecutively by $\psi_i(\boldsymbol{x})$ and integrate over Ω; keeping only linear terms with respect to $\boldsymbol{c}^s(t) = (c_s^1(t), \dots, c_s^n(t))$, $s = 1, 2, \dots$, we obtain the linear systems of equations of the form

$$\frac{d\boldsymbol{c}^s(t)}{dt} = \boldsymbol{W}(\boldsymbol{A} - \lambda_s \boldsymbol{D})\boldsymbol{c}^s(t), \quad s = 1, 2, \dots, \tag{4.6}$$

where $\boldsymbol{W} = \operatorname{diag}(w_1, \dots, w_n)$ and $\boldsymbol{D} = \operatorname{diag}(d_1, \dots, d_n)$. By the assumptions of the theorem, the trivial solution to (4.6) is asymptotically stable. To prove this fact, it is sufficient to consider a Lyapunov function $V_s(t) = \langle \boldsymbol{W}^{-1}\boldsymbol{c}^s(t), \boldsymbol{c}^s(t)\rangle$ and use the properties of the spectrum of the problem (3.5).

Putting together the last two observations we obtain that choosing δ small enough in (4.2) yields that

$$\|v_k(\boldsymbol{x}, t) - w_k\|_{L^2(\Omega)} < \varepsilon, \quad t \geq 0, \quad k = 1, \dots, n.$$

This implies that the asymptotic stability (instability) of the interior solution to (2.7) coincides with asymptotic stability (instability) of the interior solution to (3.4). □

Corollary 4.2. *Let μ_K be the maximal real part of the eigenvalues of the matrix $\boldsymbol{A}_K$, which is obtained from $\boldsymbol{A}$ by removing rows and columns with the indexes from the set $K \subset \{1, \dots, n\}$ and let $\boldsymbol{w} \in \operatorname{bd} S_n$ be a rest point of* (2.12) *such that $w_i = 0$ if $i \in K$. Then if the condition* (3.8) *is satisfied with μ_K instead of μ, then the asymptotic stability (instability) of $\boldsymbol{w}$ implies the asymptotic stability (instability) of these solutions as stationary points of* (2.7).

More can be said if we consider the notion of stability in the sense of the mean integral value (for the exact definition see [6]), which describes the stability of the averaged solutions

$$\overline{v}_k(t) = \int_\Omega v_k(\boldsymbol{x}, t)\, \mathrm{d}\boldsymbol{x}.$$

The stability in the sense of the mean integral value follows from the usual Lyapunov stability, whereas the opposite is not true (see [6]).

Corollary 4.3. *Let the reaction–diffusion replicator equation* (2.4)–(2.8) *have μ-resonant diffusion coefficients, where μ is the maximal real part of the eigenvalues of $\boldsymbol{A}$, then the asymptotic stability (instability) of $\boldsymbol{w} \in S_n$ of the problem* (2.12) *implies asymptotic stability (instability) of $\boldsymbol{u}(\boldsymbol{x})$ of the problem* (2.4)–(2.8) *in the sense of the mean integral value.*

Proof. Let us look for the solution to (2.4)–(2.8) in the form

$$v_k(\boldsymbol{x}, t) = \overline{u}_k + c_k^0(t) + \sum_{s=1}^{\infty} c_s^k \psi_s(\boldsymbol{x}), \quad k = 1, \dots, n,$$

such that $|\overline{v}_k(t) - \overline{u}_k| = |c_k^0(0)| < \delta$, for some $\delta > 0$. Corollary 3.4 yields that the mean integral values $\overline{u}_k$ of the spatially nonuniform solutions $u_k(\boldsymbol{x})$ are the stationary points of the replicator equation (2.12). Therefore, $\overline{u}_k = w_k$, where $\boldsymbol{w}$ solves (3.4). Note that (4.4) holds, and for $c_k^0(t)$ we obtain the linear approximation (4.5), therefore, if $\boldsymbol{w}$ is asymptotically stable, then $c_k^0(t)$ tend to 0 and $\boldsymbol{u}(\boldsymbol{x})$ is asymptotically stable in the sense of the mean integral value. □

5. Replicator dynamics

Prior to stating the main theorem here, we give a definition of persistence (e.g., [7]) and recall the specific form of Poincaré's inequality that we use.

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Definition 5.1. The replicator equation defined on the integral simplex $S_n(\Omega_t)$ is said to be persistent if the initial conditions (2.8) $\overline{\varphi}_k > 0$ for $k = 1, \dots, n$ imply

$$\liminf_{t\to\infty} \overline{v}_k(t) > 0, \quad k = 1, \dots, n, \tag{5.1}$$

where

$$\overline{v}_k(t) = \int_\Omega v_k(\boldsymbol{x}, t)\, \mathrm{d}\boldsymbol{x}.$$

We will use Poincaré's inequality in the following form (see [24]). Let $g(\boldsymbol{x}) \in W^{r,2}$, $r = 1, 2$. There exist nonnegative constants c_1 and c_2, which depend on the geometry of Ω and do not depend on $g(\boldsymbol{x})$, such that

$$\int_\Omega g^2(\boldsymbol{x})\, \mathrm{d}\boldsymbol{x} \le c_1 \int_\Omega \|\nabla g(\boldsymbol{x})\|^2\, \mathrm{d}\boldsymbol{x} + c_2 \Big(\int_\Omega g(\boldsymbol{x})\, \mathrm{d}\boldsymbol{x} \Big)^2.$$

In the particular case when $\int_\Omega g(\boldsymbol{x})\, \mathrm{d}\boldsymbol{x} = 0$ we have

$$\int_\Omega g^2(\boldsymbol{x})\, \mathrm{d}\boldsymbol{x} \le c_1 \int_\Omega \|\nabla g(\boldsymbol{x})\|^2\, \mathrm{d}\boldsymbol{x}, \tag{5.2}$$

and $c_1 = \lambda_1^{-1}$, where λ_1 is the minimal nonzero eigenvalue of the problem (3.5).

Theorem 5.2. *Assume that*

$$\lambda_1 d_{\min} \ge \mu, \quad d_{\min} = \{d_1, \dots, d_n\}, \tag{5.3}$$

and μ is the spectral radius of $\boldsymbol{A}$. If there exists a vector $\boldsymbol{p} \in \operatorname{int} S_n$ for which

$$\langle \boldsymbol{A}\boldsymbol{w}, \boldsymbol{p} \rangle - \langle \boldsymbol{A}\boldsymbol{w}, \boldsymbol{w} \rangle \ge 0 \tag{5.4}$$

for all points $\boldsymbol{w} \in \operatorname{bd} S_n$, then system (2.4)–(2.8) is persistent.

Proof. Consider a functional, depending on the variable t, on the set $S_n(\Omega_t)$,

$$F(\boldsymbol{v}) = F\big(\boldsymbol{v}(\boldsymbol{x}, t)\big) = \exp\Big(\sum_{k=1}^n p_k \overline{\log v_k}(\boldsymbol{x}, t) \Big), \quad \boldsymbol{v}(\boldsymbol{x}, t) \in S_n(\Omega_t),$$

where $\boldsymbol{p} \in \operatorname{int} S_n$,

$$\overline{\log v_k}(\boldsymbol{x}, t) = \int_\Omega \log v_k(\boldsymbol{x}, t)\, \mathrm{d}\boldsymbol{x}.$$

Note that $F(\boldsymbol{v}) > 0$, if $\boldsymbol{v} \in \operatorname{int} S_n(\Omega_t)$.

Consider a sequence of vector-functions $\boldsymbol{v}^s(\boldsymbol{x}, t)$, $s = 1, 2, \dots$, that converges to some element $\boldsymbol{v}(\boldsymbol{x}, t) \in \operatorname{bd} S_n(\Omega_t)$, $t > 0$. Hence for some indices $k \in K$ we have

$$\overline{v}_k^s(t) = \int_\Omega v_k^s(\boldsymbol{x}, t)\, \mathrm{d}\boldsymbol{x} \to 0, \quad s \to \infty,\ k \in K.$$

By Jensen's inequality (e.g., [24])

$$\overline{\log v_k}(\boldsymbol{x}, t) \le \log \overline{v}_k(t), \quad k = 1, \dots, n.$$

From the convergence of $\overline{v}_k^s(t)$ to zero and the last inequality we have

$$F\big(\boldsymbol{v}^s(\boldsymbol{x}, t)\big) \le \exp\Big(\sum_{k=1}^n p_k \log \overline{v}_k^s(t) \Big) = \prod_{k=1}^n \Big(\overline{v}_k^s(t) \Big)^{p_k} \to 0,$$

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for $\boldsymbol{p} \in \operatorname{int} S_n$. Therefore $F(\boldsymbol{v})$ is equal to zero on the set $\operatorname{bd} S_n(\Omega)$.

We also note that

$$\frac{d}{dt}F(\boldsymbol{v}) = \dot{F}(\boldsymbol{v}) = F(v)\sum_{k=1}^{n} p_k \dot{\overline{\log v_k}}(\boldsymbol{x},t),$$

where the dot denotes the derivative with respect to time.

Rewrite the reaction–diffusion replicator equation (2.7) as

$$\frac{\partial}{\partial t}\log v_k(\boldsymbol{x},t) = \big(\boldsymbol{A}\boldsymbol{v}(\boldsymbol{x},t)\big)_k - f^{sp}(t) + d_k \Delta v_k(\boldsymbol{x},t), \quad k = 1,\dots,n, \quad \boldsymbol{v} \in \operatorname{int} S_n(\Omega_t).$$

On integrating with respect to $\boldsymbol{x} \in \Omega$ we have

$$\dot{\overline{\log v_k}}(\boldsymbol{x},t) = \big(\boldsymbol{A}\overline{\boldsymbol{v}}(t)\big)_k - f^{sp}(t), \quad k = 1,\dots,n.$$

Therefore,

$$\dot{F}(\boldsymbol{v}) = F(\boldsymbol{v})\big(\langle \boldsymbol{A}\overline{\boldsymbol{v}}(t), \boldsymbol{p}\rangle - f^{sp}(t)\big). \tag{5.5}$$

Consider the representation

$$v_k(\boldsymbol{x},t) = \overline{v}_k(t) + V_k(\boldsymbol{x},t), \quad k = 1,\dots,n, \tag{5.6}$$

where

$$\overline{v}_k(t) = \int_\Omega v_k(\boldsymbol{x},t)\,d\boldsymbol{x}, \quad V_k(\boldsymbol{x},t) = \sum_{s=1}^{\infty} c_s^k(t)\psi_s(\boldsymbol{x}).$$

From (5.6) it follows that

$$f^{sp}(t) = \langle \boldsymbol{A}\overline{\boldsymbol{v}}(t), \overline{\boldsymbol{v}}(t)\rangle + \int_\Omega \langle \boldsymbol{A}\boldsymbol{V}(\boldsymbol{x},t), \boldsymbol{V}(\boldsymbol{x},t)\rangle\,d\boldsymbol{x} - \sum_{k=1}^{n}\int_\Omega d_k \|\nabla V_k(\boldsymbol{x},t)\|^2\,d\boldsymbol{x}. \tag{5.7}$$

Since

$$\int_\Omega V_k(\boldsymbol{x},t)\,d\boldsymbol{x} = 0, \quad k = 1,\dots,n,$$

by Poincaré's inequality (5.2) we have

$$\lambda_1 \int_\Omega \big(V_k(\boldsymbol{x},t)\big)^2\,d\boldsymbol{x} \le \int_\Omega \|\nabla V_k(\boldsymbol{x},t)\|^2\,d\boldsymbol{x},$$

where λ_1 is the first nonzero eigenvalue of the problem (3.5).

If μ is the spectral radius of $\boldsymbol{A}$, then

$$|\langle \boldsymbol{A}\boldsymbol{V}(\boldsymbol{x},t), \boldsymbol{V}(\boldsymbol{x},t)\rangle| \le \mu \sum_{k=1}^{n} |V_k(\boldsymbol{x},t)|^2.$$

As a result, from (5.7) we have

$$f^{sp}(t) \le \langle \boldsymbol{A}\overline{\boldsymbol{v}}(t), \overline{\boldsymbol{v}}(t)\rangle + \sum_{k=1}^{n}(\mu - d_k\lambda_1)\int_\Omega \big(V_k(\boldsymbol{x},t)\big)^2\,d\boldsymbol{x}.$$

If (5.3) holds then

$$f^{sp}(t) \le \langle \boldsymbol{A}\overline{\boldsymbol{v}}(t), \overline{\boldsymbol{v}}(t)\rangle, \tag{5.8}$$

therefore (5.5) yields

$$\dot{F}(\boldsymbol{v}) \ge F(\boldsymbol{v})\big(\langle \boldsymbol{A}\overline{\boldsymbol{v}}(t), \boldsymbol{p}\rangle - \langle \boldsymbol{A}\overline{\boldsymbol{v}}(t), \overline{\boldsymbol{v}}(t)\rangle\big). \tag{5.9}$$

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Let us use Remark 2.3 and identify $\boldsymbol{v}(\boldsymbol{x},t) \in \operatorname{bd} S_n(\Omega_t)$ with a $\boldsymbol{w}(t) \in \operatorname{bd} S_n$ such that $\boldsymbol{w}(t) = \overline{\boldsymbol{v}}(t)$

From inequality (5.9) it follows that

$$F(\boldsymbol{v}) \geq C \exp\Big\{ \int_0^t \big(\langle \boldsymbol{A}\overline{\boldsymbol{v}}(t), \boldsymbol{p}\rangle - \langle \boldsymbol{A}\overline{\boldsymbol{v}}(t), \overline{\boldsymbol{v}}(t)\rangle \big)\, \mathrm{d}t \Big\},$$

where $C = F(\boldsymbol{v})|_{t=0}$.

Assume that there exists a $t > 0$ such that $\boldsymbol{v}(\boldsymbol{x},t) \in \operatorname{bd} S_n(\Omega_t)$. Then $F(\boldsymbol{v}) = 0$. On the other hand, using Remark 2.3, we can identify any $\boldsymbol{v}(\boldsymbol{x},t) \in \operatorname{bd} S_n(\Omega_t)$ with $\boldsymbol{w}(t) \in \operatorname{bd} S_n$, then, using (5.4), we must have

$$F(\boldsymbol{v}) \geq C > 0,$$

which proves that the system is persistent. □

Remark 5.3. To validate condition (5.4) is an independent algebraic problem.

Here is one possible approach. Assume that the vector $\left(\boldsymbol{A}^\top\right)^{-1}\mathbf{1}$ is positive. Here $\mathbf{1} = (1,\dots,1)^\top \in \mathbf{R}^n$. Consider $\boldsymbol{p} \in \operatorname{int} S_n$

$$\boldsymbol{p} = \frac{\left(\boldsymbol{A}^\top\right)^{-1}\mathbf{1}}{\langle \left(\boldsymbol{A}^\top\right)^{-1}\mathbf{1}, \mathbf{1}\rangle}.$$

For any $\boldsymbol{w} \in \operatorname{bd} S_n$, one has

$$\langle \boldsymbol{A}\boldsymbol{w}, \boldsymbol{p}\rangle = \frac{1}{\langle \left(\boldsymbol{A}^\top\right)^{-1}\mathbf{1}, \mathbf{1}\rangle}.$$

On the other hand

$$\langle \boldsymbol{A}\boldsymbol{w}, \boldsymbol{w}\rangle \leq \mu \langle \boldsymbol{w}, \boldsymbol{w}\rangle,$$

where μ is the spectral radius of $\boldsymbol{A}$. Since $\langle \boldsymbol{w}, \boldsymbol{w}\rangle \leq 1$ for any $\boldsymbol{w} \in \operatorname{bd} S_n$, then the inequality

$$\mu < \frac{1}{\langle \left(\boldsymbol{A}^\top\right)^{-1}\mathbf{1}, \mathbf{1}\rangle}$$

yields the condition (5.4).

To illustrate this approach, consider a very simple example.

Example 5.4. Consider the following replicator system with the global regulation of the second kind

$$\begin{aligned} \partial_t u_1 &= u_1(\beta u_1 + k_2 u_2 - f^{sp}(t) + d_1 \Delta u_1), \\ \partial_t u_2 &= u_2(k_2 u_1 - f^{sp}(t) + d_2 \Delta u_2), \end{aligned} \tag{5.10}$$

$\boldsymbol{x} \in \Omega$ and $\partial_\nu u_i = 0$, $\boldsymbol{x} \in \Gamma$. Using the approach outlined above, we obtain

$$p_1 = \frac{k_1}{k_1 + k_2 - \beta}, \quad p_2 = \frac{k_2 - \beta}{k_1 + k_2 - \beta}.$$

The condition (5.4) takes the form

$$(k_1 w_2 + \beta w_1) p_1 + k_2 w_2 p_2 - (k_1 + k_2) w_1 w_2 - \beta w_1^2 > 0.$$

This is obviously true for $w_1 = 0$, $w_2 = 1$. For the case $w_1 = 1$, $w_2 = 0$ we have

$$\frac{\beta k_1 - (k_1 + k_2)\beta + \beta^2}{k_1 + k_2 - \beta} > \frac{\beta^2 - k_2 \beta}{k_1 + k_2 - \beta}.$$

The last expression will be positive if we require $k_1 > \beta > k_2$. Finally, consider, e.g., the square $\Omega = (0,1) \times (0,1)$. In this area the condition (5.3) yields

$$d_{\min} \geq \frac{\beta + \sqrt{\beta^2 + 4k_1 k_2}}{8\pi^2}.$$

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The estimate in Theorem 5.2 gives only sufficient condition, as it can be seen, for instance, from the hypercycle replicator equation with the matrix

$$\boldsymbol{A} = \begin{bmatrix} 0 & 0 & \dots & 0 & a_1 \\ a_2 & 0 & \dots & 0 & 0 \\ 0 & a_3 & 0 & \dots & 0 \\ \vdots & \ddots & \ddots & & \vdots \\ 0 & \dots & 0 & a_n & 0 \end{bmatrix}.$$

It is well known that the hypercyclic system is persistent [15], i.e., the variables are separated from zero by a positive constant. Condition (5.4) holds only for the short hypercycles ($n = 2, 3, 4$). Indeed, for $n = 2$ we have $\langle \boldsymbol{A}\boldsymbol{w}, \boldsymbol{w}\rangle = (a_1 + a_2)w_1 w_2 = 0$, $\boldsymbol{w} \in S_n$. For $n = 3$ (5.4) holds if we choose

$$p_i = \frac{a_i^{-1}}{R_3}, \quad i = 1, 2, 3, \quad R_3 = \sum_{j=1}^{3} \frac{1}{a_j}, \quad \text{and } R_3 = \max\{a_1, a_2, a_3\} \le 4, \quad i = 1, 2, 3.$$

Condition (5.3) yields here

$$d_{\min} \ge \frac{(a_1 a_2 a_3)^{1/3}}{\lambda_1}.$$

For the $n = 4$ (5.4) will hold for a similar choice of $\boldsymbol{p}$ only for $a_1 = a_2 = a_3 = a_4$.

6. Numerical analysis of a particular replicator system

In this section we present an example which possesses the following feature: The non-distributed replicator equation is shown to be non-persistent (for the chosen parameter values three members of a catalytic network go extinct), whereas the distributed replicator equation with the global regulation of the second kind is persistent (for the same parameter values all six members of the catalytic network are subject to time dependent oscillations).

Consider a replicator system with the matrix

$$\boldsymbol{A} = \begin{bmatrix} 0 & 0 & \alpha & 0 & 0 & \gamma \\ \alpha & 0 & 0 & 0 & \gamma & 0 \\ 0 & \alpha & 0 & \gamma & 0 & 0 \\ \gamma & 0 & 0 & \beta & 0 & 0 \\ 0 & 0 & \gamma & 0 & \beta & 0 \\ 0 & \gamma & 0 & 0 & 0 & \beta \end{bmatrix}. \tag{6.1}$$

The catalytic network which corresponds to the interaction matrix (6.1) presented in Fig. 1a. This particular cooperative network, which contains two catalytic cycles, is based on the in vitro network of RNA molecules, which was shown to be capable of sustained self-replication [25]. We note that we were not able to infer the reaction rates from [25], therefore the only ingredient that was inspired by [25] is the exact form of the catalytic network. An important fact for us is that, according to [25], there exist such reaction rates α, β, γ for which all six members of the catalytic network survive and evolve.

Our task is to compare the behavior of solutions of three different analytical approaches to model this network: Classical local replicator equation (2.12), reaction–diffusion replicator equation with the global regulation of the first kind (2.9) and reaction-diffusion replicator equation with the global regulation of the second kind (2.7).

Let the parameters take the values

$$\alpha = 1.75, \quad \beta = 0.7, \quad \gamma = 2.0.$$

For these parameter values it can be shown that there are fifteen rest points of (2.12) belonging to S_n, including one isolated rest point in $\operatorname{int} S_n$. However, this interior rest point is unstable. Moreover,

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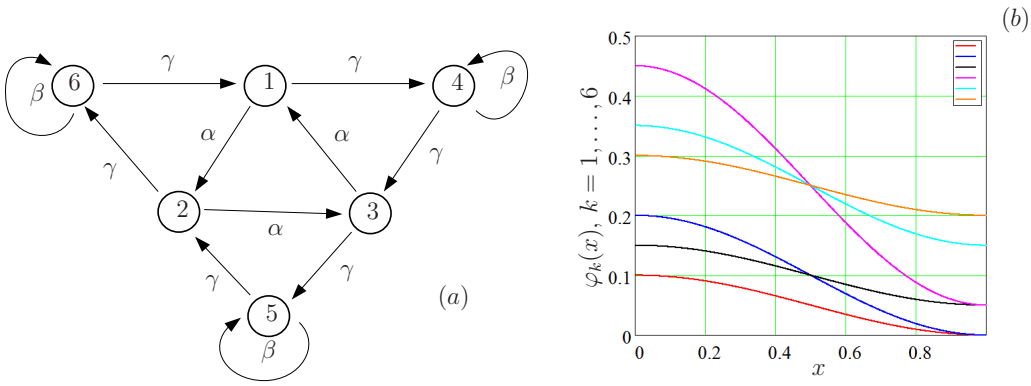


FIGURE 1. (a) A catalytic network of macromolecules. There are six macromolecules. The arrows show the catalytic activity of the molecules. The coefficients are the corresponding rate constants. This network is inspired by the catalytic network of self-replicating RNA molecules, which was shown to be capable of sustained replication [25]. (b) Initial conditions for solving problems (2.7) and (2.9) on $\Omega = (0, 1)$

numerical experiments show that there are stable rest points such that three coordinates stay positive whereas other three species go extinct. In general, the conclusion is that for the taken parameter values the system is not persistent and cannot guarantee survival of all the molecules. We do not give illustrations here because the distributed model with the global regulation of the first kind shows very similar behavior (in full accordance with the theoretical analysis in [6]).

Now consider the replicator equation with the global regulation of the first kind (2.9) on $\Omega = (0, 1)$ with Neumann's boundary conditions. The initial conditions for all the subsequent calculations are shown in Fig. 1b. The details of the numerical scheme are discussed elsewhere [4].

We take two different vectors of the diffusion coefficients: $\boldsymbol{d}_1 = (0.4, 0.5, 0.4, 0.5, 0.4, 0.5)$, $\boldsymbol{d}_2 = (0.04, 0.05, 0.04, 0.05, 0.04, 0.05)$. As it was proved in [6], for larger diffusion coefficients the system is actually becomes spatially homogeneous for sufficiently large t. For example, in Fig. 2a it is sufficient to take $t = 60$; by this time moment the distributions of the species are spatially uniform. Fig. 2b shows the time evolution for the mean values of the variables

$$\overline{v}_i(t) = \int_\Omega v_i(\boldsymbol{x}, t)\,\mathrm{d}x, \quad i = 1, \ldots, 6.$$

It can be seen that after the initial transitory period, the solutions actually attracted to the spatially homogeneous (left panel) stationary state, which corresponds exactly to the asymptotically stable rest point of the non-distributed replicator equation (2.12). For smaller diffusion coefficients $\boldsymbol{d}_2$ spatially nonhomogeneous stationary solutions appear (see Fig. 2c).

However, in the average, the behavior is still qualitatively similar to that of the homogeneous system: Three macromolecules persist whereas three others disappear from the system, which can be seen from the dynamics of the average values of the variables $\overline{v}_i(t)$ in Fig. 2b,d.

As it was proved in [6], in the sense of the average behavior, we cannot expect qualitatively different behavior from the distributed replicator equation with the global regulation of the first kind. A quite different picture is observed in the case of the reaction–diffusion replicator equation with the global regulation of the second kind (2.7). In particular, when the diffusion coefficients are large enough, the solution behavior corresponds to the non-distributed case (as was proved in Sections 3 and 4). In Fig. 3 it can be seen that, as well as in the previously discussed case of the global regulation of the first kind, there is an asymptotically stable spatially homogeneous stationary state, at which three macromolecules approach non-zero concentrations, whereas three others go extinct (cf. Figs. 2a,b and 3a,b). Decreasing

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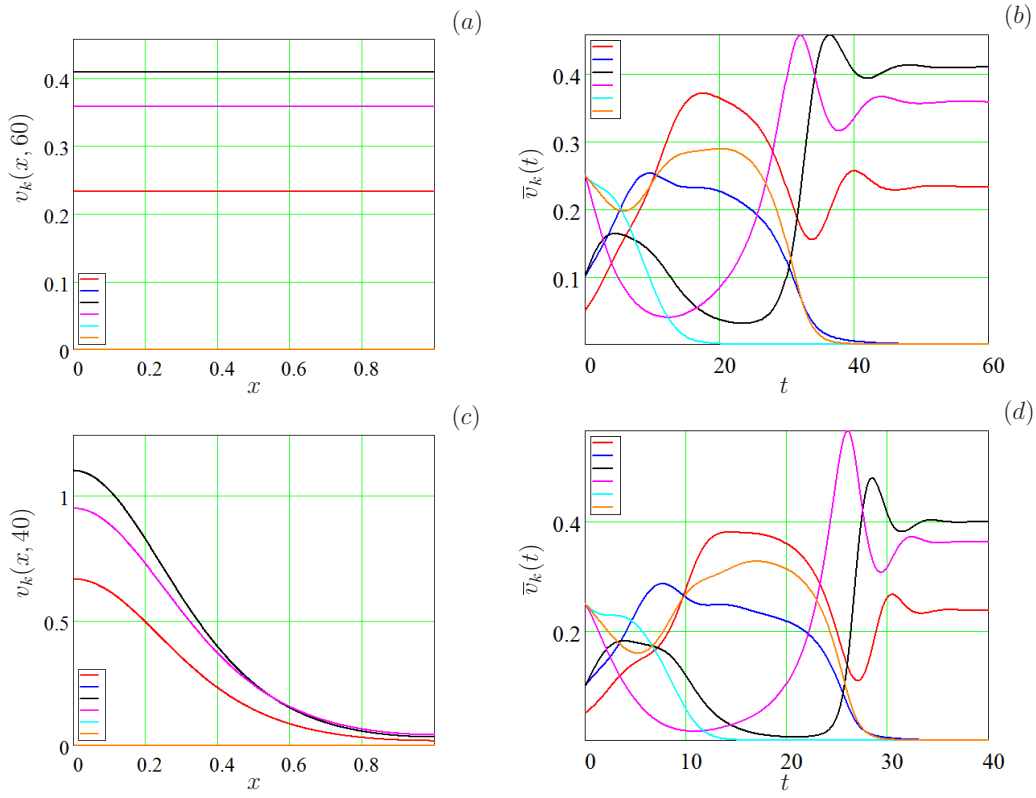


FIGURE 2. Solutions to the replicator equation with the global regulation of the first kind (2.9) on $\Omega = (0, 1)$ with interaction matrix (6.1) and with diffusion coefficients $\boldsymbol{d}_1 = (0.4, 0.5, 0.4, 0.5, 0.4, 0.5)$. (a) Solutions at the moment $t = 60$. (b) The averages of the solutions $\overline{v}_i(t)$, $i = 1, \ldots, 6$ depending on time t. (c) Solutions at the moment $t = 40$ of the same system with diffusion coefficients $\boldsymbol{d}_2 = (0.04, 0.05, 0.04, 0.05, 0.04, 0.05)$. (d) The averages of the solutions $\overline{v}_i(t)$, $i = 1, \ldots, 6$ depending on time t from (c)

the diffusion coefficients yields a qualitative change in the system behavior. Firstly, the solutions do not seem to approach a spatially uniform stationary state, the numerical calculations suggest that they keep oscillating. Secondly and most importantly, we observe that the concentrations of all six macromolecules are separates from zero, the system becomes persistent (see Fig. 3c,d).

In Fig. 4 time dependent solutions in the space (x, t) are shown that correspond to the case of Fig. 3d.

In conclusion we note that the important phenomena observed numerically in this section call for analytical proofs, and this is one of our ongoing projects to supplement the numerical findings of the current text with analytical theory.

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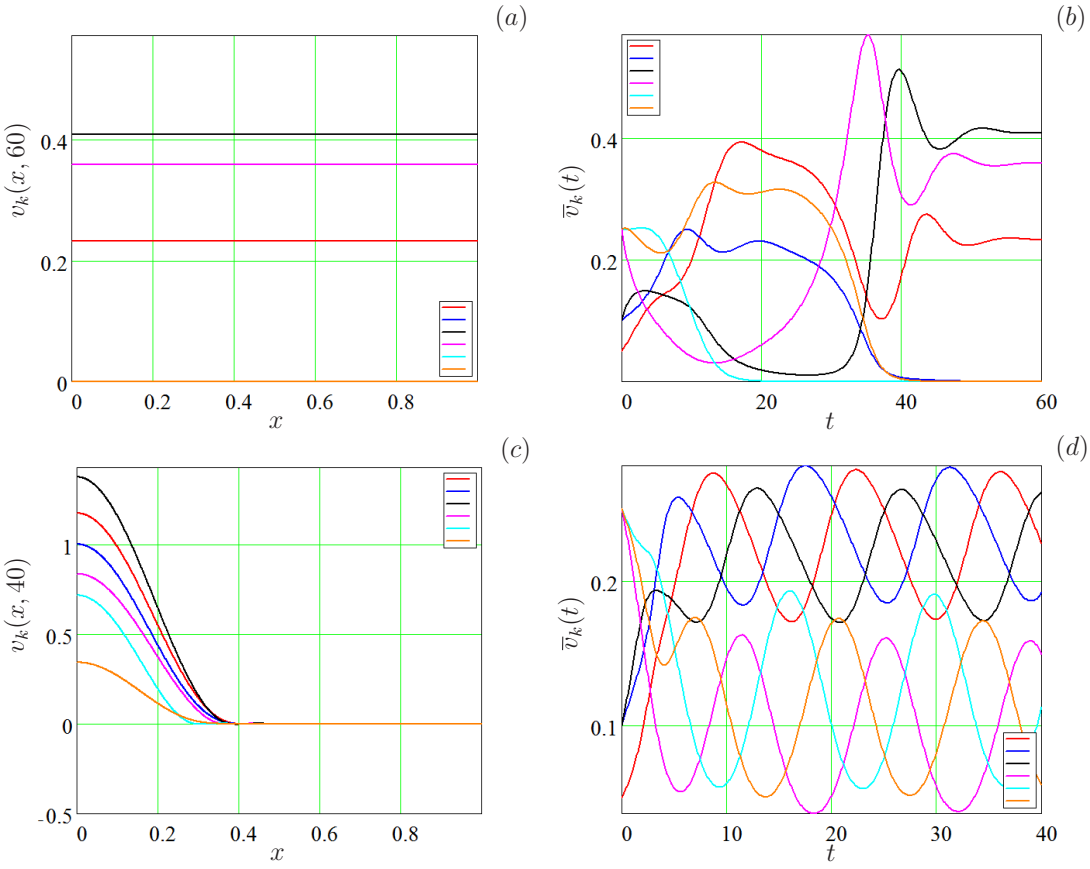


FIGURE 3. Solutions to the replicator equation with the global regulation of the second kind (2.7) on $\Omega = (0,1)$ with interaction matrix (6.1) and with diffusion coefficients $\boldsymbol{d}_1 = (0.4, 0.5, 0.4, 0.5, 0.4, 0.5)$. (a) Solutions at the moment $t = 60$. (b) The averages of the solutions $\overline{v}_i(t)$, $i = 1, \ldots, 6$ depending on time t. (c) Solutions at the moment $t = 40$ of the same system with diffusion coefficients $\boldsymbol{d}_2 = (0.04, 0.05, 0.04, 0.05, 0.04, 0.05)$. (d) The averages of the solutions $\overline{v}_i(t)$, $i = 1, \ldots, 6$ depending on time t from (c)

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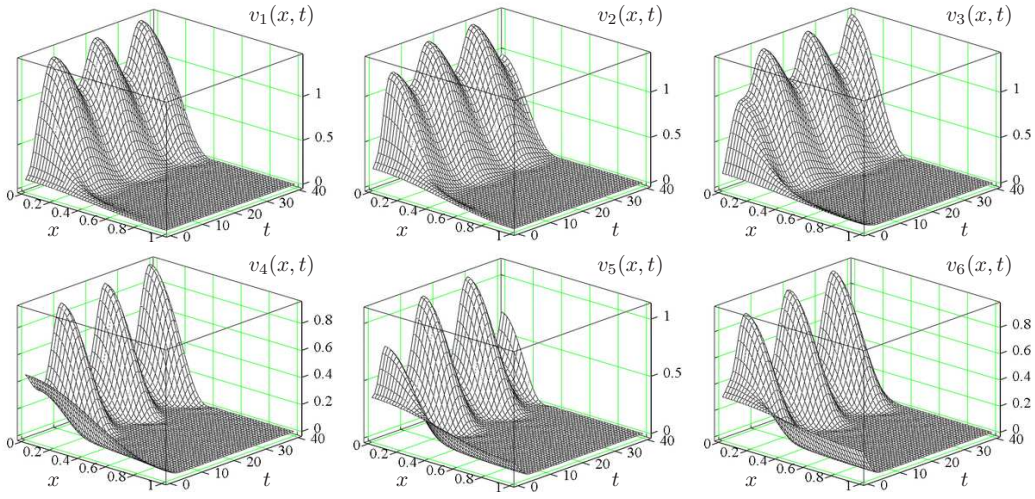


FIGURE 4. Solutions in the (x,t) space to the problem (2.7) on $\Omega = (0,1)$ with interaction matrix (6.1) and with diffusion coefficients $\boldsymbol{d}_2$. The averaged values of the variables $\overline{v}_i(t)$ are shown in Fig. 3d

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