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The use of evolution optimality principles in simulation of structured biosystems

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Abstract — Approaches to use the theory of evolutionary optimality in the study of structured models of biological communities are proposed. Relations of this theory to the stability of equilibrium states are indicated and the formulation of its main result for the case of a quasilinear dynamical systems in normed spaces is presented. For models of communities with age, spatial, and age-spatial structure, functionals optimized over parameters of evolutionary selection are constructed. The functionals are calculated on the basis of the available information concerning steady stationary distributions. The sets of parameters obtained as the result of this optimization can serve for identification of models.

Keywords: Evolution optimality principle, age-dependent systems, spatially structured systems.

Extreme principles in biology arise as a formalization of the idea of evolution and its consequence, the evolutionary optimality, originating from the fundamental work of Darwin [3]. The fact that the competition in conditions of limited living space leads to elimination of all varieties except for a small number of those most accommodated to given environmental conditions allows us to construct fundamental principles of functioning of biological systems.

Initially, the theory of optimal biological structures was considered as an independent branch of biological science based on very solid empirical basis. A high efficiency of relatively simple ideas of optimality promoted these ideas to become in their time a key principle of world order and to be reflected in a variety of widespread teleological concepts. The research of Hess [7] who considered blood circulation is regarded as one of the first scientific works concerning the use of optimality ideas for particular applied problems. Later, more detailed models of optimal structural-functional organization had been constructed just for this process [1, 2, 12]. Similar studies were undertaken for the processes of external respiration [10, 14, 23]. All these researches illustrate the diversity of used optimality criteria having in any case an energy basis.

The consideration of evolutionary selection could not leave outside the scope for a long time such characteristics of organisms that are most directly involved in the processes related to the change of generations. As the result, along with the criteria developed previously, new criteria had been developed on the base of the influence imposed by considered biological structure on the reproductive function. The cri-

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teria of Fisher [5] and Haldane (see [25]) are among the most known of them. The accumulated experience in the use of mathematical models based on the optimality principle had led to the hypothesis about the universality of this principle in biology which in the context of its relationship with evolutionary selection had found its representation in the 'principle of adequate structures' of Rashevsky [17]. In the formulation of Rosen [24] this principle is read as 'Organisms possessing biological structure that is optimal with respect to natural selection are also optimal in the sense that they minimize a certain value function defined on the base of characteristics of the environment'. In the same Rosen's monograph one can find a detailed overview of the results of application of the optimality principle in biology for all its half-century history. Many structural and functional parameters concordant with actual observed values were determined on the basis of this principle. Among them are diameters and branching angles of bronchi vessels, blood throughput rate in the circulatory system, etc. The discussion of these results, as well as many others, can be found in [8, 13], and also in [15].

From the viewpoint of mathematical justification of principles used for solution of practical problems, the most interesting are papers [6, 25] where a clear relationship between the stability of steady equilibrium states corresponding to the final stage of the evolutionary process and extremal properties of values of Malthusian functions calculated in such equilibrium states and corresponding to surviving species (i.e., those with nonzero size, see next section). In the context of these publications, the principle of optimality had got in biology the name of 'principle of evolution optimality', which is quite clear in the mathematical sense. However, despite the depth and serious mathematical basis of these works, the range of their application remained extremely narrow until recently. The operation with total population sizes was often inadequate to reality because of the differences of population roles of juvenile and adult individuals. A similar problem occurred regarding to spatially distributed biological communities. Natural systems endowed with one or another continuous structure (and first of all the age system) fell out in mass from consideration. This was mainly caused by the complexity of mathematical technique necessary for strict construction of the theory taking into account properties of dynamical system in spaces of distributions. Researches implemented at the so-called 'physical level of strictness' appeared from time to time, in the context of distribution dynamics problems this meant a neglect of fundamental mathematical issues caused by a specific character of unbounded operators determining such dynamical systems. As an example of a gap appearing in consideration at this level we may indicate the neglect of the presence of operator spectrum components except for its discrete part and, as a rule, the latter is considered by default as a set of simple eigenvalues. For example, we may rank monograph [4] as one of such works, it posed the problem of evolutionary optimality for a system with continuous age structure. The existence of such publications creates a general understanding of the nature of evolutionary selection processes in distributed biological systems, but does not change the overall picture of gaps in the theory because they do not contain any acceptable justification of the principles proposed there from the mathematical point of view.

The theory constructed by the author (see [18, 19]) makes an attempt to overcome the shortcomings indicated above and propose a construction combining the stability properties of stationary modes of distributed biological systems with extreme properties of values of inherited traits in species surviving in these modes. Without going into details, note that despite some artificial nature (the quasi-linear nature of problems with continuous time specifies a number of technical, but quite natural restrictions) this theory allows us to obtain interesting and practically useful results in some urgent cases. An overview of most marked of them is offered to the reader in this paper.

The second section of this paper reveals the main idea of the theory of evolutionary optimality at the level of point systems. Methodologically, it has a propaedeutic character, in essence it has a historical sense. This section presents the simplest point mathematical model being widely known as classic and elementary helping in clarification of the nature of the ideas arising from the relationship of stability and evolutionary optimality. Malthusian functions are optimized in this model and these functions play the role of 'lighthouses' in construction of functionals for more complex systems.

In the third section we formulate a key theorem of the general abstract theory and also its corollary in the form of an extreme principle for the real part of the spectrum of the operator entering the original system.

The fourth section presents applications of the theory to systems of equations describing communities of biological populations with continuous age structure. In this case, a functional constructed in a special manner (reproduction potential of the population) is optimized, and this functional is calculated through original functions.

The fifth section contains applications of the theory to spatially distributed biological systems. The basic model here is a system of 'reaction–diffusion' type equations with coefficients of diffusion not dependent on phase variables. In this case right-hand sides of equations can contain bounded functions dependent not only on values of phase variables, but also on some spatial functionals of those variables. A certain 'energy' functional of spatial variables is optimized here.

The sixth section combines two preceding ones. We specify particular conditions that help us to construct easily the functional for systems of interacting species endowed with both the spatial and age structure. The structure of optimal distributions having separated spatial and age profiles is presented.

1. The principle of evolutionary optimality

The tendencies of natural selection in competition at intersections of ecological niches lead in time corresponding to stabilization of processes to formation of structures that can be considered as stabilized (stable in mathematical terminology). Taking the simplest model of interaction of n biological species

$$\frac{\mathrm{d}x_i}{\mathrm{d}t} = x_i f_i(x), \quad i = 1,\dots,n, \quad x = (x_1,\dots,x_n) \tag{1.1}$$

as an example, we obtain the necessary stability condition for the equilibrium state $\bar{x} = (\bar{x}_1, \ldots, \bar{x}_m, 0, \ldots, 0)$; $\bar{x}_i > 0$, $i = 1, \ldots, m$, representing the species structure of a community containing only first m species from all possible ones in the form of the equality

$$f_i(\bar{x}) = \max_j \{f_j(\bar{x})\}, \quad 1 \leqslant i \leqslant m, \quad 1 \leqslant j \leqslant n. \tag{1.2}$$

For $x = \bar{x}$ the Jacobian of system (1.1) has the following block structure:

$$\left(\frac{\partial (x_i f_i(x))}{\partial x_j} \right) \Bigg|_{x=\bar{x}} = \begin{pmatrix} A & B \\ 0 & D \end{pmatrix}$$

with a diagonal $(n-m) \times (n-m)$ matrix D having nonpositive elements $f_j(\bar{x})$, $j > m$, on the main diagonal because of assumed stability and $f_j(\bar{x}) = 0,\ j \leqslant m$.

Equality (1.2) has a character of an extremal relation and expresses the *principle of evolutionary optimality*. Its biological sense is that the species survived in the equilibrium state must have maximal values of the Malthusian functions calculated in this state relative to all potentially admissible species. Just these parameters characterize the strength of species in its Darwinian sense if we have in mind the heuristic formulation of the rule on survival of the strongest.

Since in the equilibrium state $\bar{x}$ the species with the numbers $m+1 \leqslant j \leqslant n$ are absent, we can assume them virtual, i.e., we can add to them any other species having a hypothetical possibility to be in the original set. In this case, the numbers marking the species are not necessarily taken from a certain finite set, as in the example considered above, but may have an arbitrary nature. In particular, those marks can be taken as elements of some (usually bounded) domain Λ of a finite-dimensional (and probably an infinite-dimensional as some class of functions) space so that optimization problem (1.2) will be solved subject to this domain. (For this reason, instead of the term ‘number’ in the context of this paper we can use its synonym ‘parameter of selection’ more suitable in continuous interpretation.) This extension allows us to find isolated points in the domain Λ in the typical case of solution of the extremal problems, and these points contain the selection parameters $\bar{\lambda} \in \Lambda$ for which the equilibrium state $\bar{x}$ is stable.

Note that in addition to necessary conditions of stability (1.2) mentioned here, responsible for *external* stability, and characterizing the stability of the equilibrium state of the community with respect to introduction of species not represented in this state, we also need an *internal* stability characterizing the stability with respect to small deviations of sizes of existing species. The determination of the values of $\bar{\lambda} \in \Lambda$ corresponding to really observed species in the given conditions (including species community structure) can be used as a methodological base for identification of those parameters of observed (quasi)stationary biological systems which determination by field measurements may be impossible or unreasonably difficult.

The greatest practical difficulty in mathematical models of specific structured biological communities is in construction of maximized functionals of distributions whose role in the considered point example is implemented by the functions of sizes $f_i(x)$. If we succeed in construction of such functionals, then analogues of the results presented above (as well as the technique of subsequent calculations) can be derived from the more general theory of interrelation of stability and optimality for the case of distributed quasilinear systems developed by the author (see [18, 19]).

2. Some results of the general theory

This section presents formulations of fundamental results of the theory joining the stability and evolutionary optimality in the models of distributed biological systems. We restrict ourselves with autonomous systems with continuous time that fit structurally into the description of quasilinear dynamic systems in Banach spaces. The proofs can be found in [18].

The original dynamic system in its autonomous formulation has the form

$$\begin{aligned} \frac{\mathrm{d}x}{\mathrm{d}t} &= (h_x + a(x,y))x \\ \frac{\mathrm{d}y}{\mathrm{d}t} &= h_y y + b(x,y) \end{aligned} \tag{2.1}$$

where $t \in J = [0,T]$, $T > 0$, $x \in X$, $y \in Y$, X, and Y are Banach spaces, $a \in C^1(X \oplus Y, B(X))$, $b \in C^1(X \oplus Y, Y)$, $B(X)$ is the space of bounded linear operators in X. The linear operators $h_{x,y}$ are taken as infinitesimal generators of strongly continuous semigroups of linear bounded operators acting in X and Y, respectively. Recall that the family of such operators $T(t)$, $t \geqslant 0$, acting in X is called a semigroup if for any $t,s \geqslant 0$ the equality $T(t+s) = T(t)T(s)$ holds. The strong continuity means the continuity of the family $T(t)x$, $t \geqslant 0$ for any $x \in X$. In this case its infinitesimal generator h_x is given for $x \in X$ as the limit $h_x x = \lim_{t \searrow 0}(T(t)x - x)/t$ with the domain of definition $D(h_x) \subset X$ for which the indicated limit exists for $x \in D(h_x)$. In particular, such operators are closed (i.e., the set $\{(x, h_x x),\ x \in D(h_x)\}$ is closed in $X \oplus X$) and have a dense domain of definition $D(h_x) \subset X$.

The variables of system (2.1) are initially divided into two following groups: x are evolutionary variables (are characterized by vanishing of their variation at zero values) and y are nonevolutionary ones (required only to achieve the generality necessary for applications; can be omitted in mathematical constructions for the sake of brevity). The shortened notation of system (2.1) is

$$\frac{\mathrm{d}w}{\mathrm{d}t} = hw + K(w)$$

where

$$w = (x,y) \in W = X \oplus Y, \qquad h = \begin{pmatrix} h_x & 0 \\ 0 & h_y \end{pmatrix}.$$

The issues of correct solvability, extension in time, positivity (construction of invariant cones), (Hölder) smoothness with respect to initial conditions were considered in details in [18]. However, some of them can be clarified from classic results (see, e.g., [16]).

In its original variant [18] the system was not autonomous and with periodic coefficients. The periodicity was required for reducing the original problem (for flows) to a simpler (with bounded operators in the right-hand side) one for cascades (in a period). The autonomous case fits into the general scheme for any positive value of the period. The stability of the stationary solution $\bar{w} = (\bar{x}, \bar{y})$ is understood for it in the sense of localization in the unit circle of the spectrum of the Jacobian for the mapping calculated in positive time in $\bar{w}$.

A projector P, i.e., a linear bounded idempotent ($P^2 = P$) operator in W is called *admissible* relative to h if its domain of definition satisfies the relation $PD(h) \subset D(h)$ and, in addition, $hP = PhP$ (i.e., the operator h has an upper triangular form in the coordinates $(P, I - P)$, where I is the identity operator in W).

A projector P in W is said to be *admissible* relative to $w \in W$ if $Pw = w$, P is admissible relative to h, commutes with I_Y (projector on Y), and for a certain neighborhood $O(w) \subset W$ the relation $v \in PW \cap O(w)$ implies $K(v) \in PW$.

The Jacobian of system (2.1) calculated in the state of equilibrium $\bar{w} = (\bar{x}, \bar{y})$ is split into the sum $l(\bar{w}) = l_0(\bar{w}) + l_1(\bar{w})$, where

$$l_0(\bar{w}) = \begin{pmatrix} h_x + a(\bar{w}) & 0 \\ 0 & 0 \end{pmatrix}.$$

If by $C_{-\delta}$, $\delta > 0$, we denote the left complex half-plane translated to the left by δ, then the result most interesting for the autonomous case of the theory of [18] (except for some generalizations aimed to a greater adequacy to biological statements) can be formulated in the following way.

Theorem 2.1. *Let* $\bar{w} = (\bar{x}, \bar{y})$ *be a stable stationary solution to system* (2.1). *In this case for any admissible relative to* $\bar{w}$ *projectors* P_1, P_2 *in* W *such that* $P_1P_2 = P_2P_1 = P_2$ *and* $P_2I_Y = P_1I_Y$ *there exists* $\delta > 0$ *such that* $\sigma((Ql_0(\bar{w}))_{QW}) \subset C_{-\delta}$.

Here $Q = P_1 - P_2$ is a projector in W, A_V is the restriction of the linear operator $A : W \to W$ onto the subspace $V \subset W$ invariant relative to it, $\sigma(A)$ is the spectrum of the operator A.

Due to (2.1), $\bar{x} \in \mathrm{Ker}\,(h_x + a(\bar{w}))$ (kernel of the operator), therefore, in the case $\bar{x} \neq 0$ interesting for applications we have the following corollary.

Corollary 2.1 extreme principle. The maximum of the upper bound for the real part of the spectrum of restrictions of the operator $h_x + a(\bar{w})$ onto $QW \oplus \{l\bar{x}\}$, $l \in \mathbf{R}$, with the stable equilibrium position $\bar{w} = (\bar{x}, \bar{y})$ is attained on the vector $\bar{x} \neq 0$ implemented in $\bar{w}$ and is equal to zero.

The assertion formulated above is a direct generalization of the necessary external stability condition presented in the previous section in the case considered here.

3. Models with continuous age structure

The original system of equations describing the dynamics of a community with species endowed with continuous age structure has the form

$$\partial x_\lambda = -m_\lambda x_\lambda, \quad \lambda \in \Lambda \tag{3.1}$$

with the boundary conditions

$$x_\lambda(0,t) = \int_0^\infty b_\lambda(a) x_\lambda(a,t)\,\mathrm{d}a, \quad \lambda \in \Lambda \tag{3.2}$$

and appropriate initial conditions. Here t denotes the time, a is the age, $\partial_t = \partial/\partial t$, $\partial = \partial_t + \partial_a$, λ is the number (possibly from an uncountable set Λ) of species with the population density in age $x_\lambda = x_\lambda(a,t)$. System (3.1)–(3.2) is assumed autonomous in time so that each of the mortality rates $m_\lambda = m_\lambda(a,x)$ of individuals of the species with the number λ is dependent only on the age a of those individuals and the values of the distribution vector $x = \{x_\rho(\cdot,t)\}$, $\rho \in \Lambda$, describing the current (i.e., for a fixed time moment t) state of the community structure. Here and below the dot instead of a distribution variable means consideration of the distribution as a whole, i.e., as an element of an appropriate functional space. In particular, this means a functional dependence of mortality rates on the state of the community as a whole. The birth rates $b_\lambda(a)$ are assumed not dependent on the current form of distributions. The study of correct solvability of such systems can be found in [26].

In application to a community with the age structure, the main result can be formulated as follows.

If system (3.1), (3.2) has a stable position of equilibrium $\bar{x} = \{\bar{x}_\lambda(a)\}$, $\lambda \in \Lambda$, then for $\bar{\lambda} \in \operatorname{supp}(\bar{x})$ (the set of values of the parameter λ where $\bar{x}_\lambda(a)$ does not vanish to identical zero) the following relation holds:

$$\varphi\left(\bar{\lambda}\right) = \max_{\lambda \in \Lambda}\left(\varphi(\lambda)\right) \tag{3.3}$$

with the functional

$$\varphi(\lambda) = \int_0^\infty b_\lambda(a) \exp\left(-\int_0^a m_\lambda(s,\bar{x})\,\mathrm{d}s\right)\mathrm{d}a. \tag{3.4}$$

From the practical viewpoint, this means that in order to determine the values of the collection of parameters λ realized for *a priori* established stationary distribution $\bar{x}$, we have to solve the optimization problem (3.3) with respect to λ for functional (3.4). Note that the maximal theoretical value of this functional equals one.

The substantial meaning of the functional (3.4) originating from basic constructions of Lotka [9] is the mean value of the number of descendants of fixed age per one parent individual of the same age.

4. Models with continuous spatial structure

The continuous model most frequently used now for spatially distributed biological communities describes such communities with the use of systems of second order quasilinear parabolic equations with homogeneous boundary condition in the considered spatial domain. If the realized stationary distribution of biological species is known *a priori*, then we can construct a minimization problem for an appropriate integral functional in order to calculate selection parameters corresponding to survived species.

The original system of equations has the form

$$\partial_t x_\lambda = h_\lambda x_\lambda + \hat{a}_\lambda(x) x_\lambda, \quad \lambda \in \Lambda \tag{4.1}$$

where $x_\lambda = x_\lambda(\xi, t)$ is the spatial density of biomass of the species with the number λ at a spatial point $\xi \in \Omega$ (here $\Omega \subset \mathbf{R}^n$ is a connected bounded domain with a sufficiently smooth boundary $\partial\Omega$ used for description of habitat of the community) at a time moment t, h_λ are elliptic operators of the form

$$h_\lambda x_\lambda = \operatorname{div}\left(A_\lambda(\xi)\left(\operatorname{grad} x_\lambda + x_\lambda \operatorname{grad} q_\lambda(\xi)\right)\right)$$

with sufficiently smooth coefficients $a_\lambda^{\iota\varkappa}(\xi), q_\lambda(\xi)$, for $\iota, \varkappa = 1, \ldots, n$, in the closure of the domain Ω, and symmetric matrices $A_\lambda(\xi) = \left\| a_\lambda^{\iota\varkappa}(\xi) \right\|$ are assumed to be uniformly positive definite in the domain Ω (i.e., $(A_\lambda(\xi)\zeta, \zeta) \geqslant k_\lambda(\zeta, \zeta) > 0$ for $\zeta \in \mathbf{R}^n \setminus \{0\}$). The divergence and gradient are calculated here in the spatial variables ξ, the standard notation $(u, v) = \sum_{i=1}^n u_i v_i$ is used here for the scalar product in $\mathbf{R}^n$. Such operators are used for the description of diffusion in the case of a nonisotropic space (relative to possible migration of individual of species with the number λ; the isotropic case corresponds to the diffusion matrix $A_\lambda(\xi)$ proportional to an identity one) and the presence of spatial translation given by the gradient vector of the potential $q_\lambda(\xi)$ (for example, in chemotaxis problems this is a specific function of attractant concentration).

The nonpercolation conditions holds on the boundary $\partial\Omega$, i.e.,

$$\left(\operatorname{grad} x_\lambda + x_\lambda \operatorname{grad} q_\lambda(\xi), A_\lambda(\xi)\nu\right)\big|_{\partial\Omega} = 0 \tag{4.2}$$

where ν is the normal vector to the boundary at the point $\xi \in \partial\Omega$. The operator $\hat{a}_\lambda(x)$ determines here the pointwise (with respect to ξ) multiplication of the function $x_\lambda(\xi, t)$ by the function (strictly speaking, functional) $a_\lambda(x(\cdot, t), \xi)$ where we have used the notation for the vector $x = x(\cdot, t) = \left\{x_\rho(\cdot, t)\right\}$, $\rho \in \Lambda$. This operator plays the role of a Malthusian function (see the second section) of the species with the number λ. The set of such operators determines both intra- and interspecific relations in the community.

In application to the considered system with spatial structure, the main result of the theory can be formulated in the following way. If system (4.1), (4.2) has a stable stationary position of equilibrium $\bar{x}$, then the following relation is valid for $\bar{\lambda} \in \operatorname{supp}(\bar{x})$:

$$\varphi(\bar{\lambda}) = \min_{\lambda \in \Lambda} \varphi(\lambda) \tag{4.3}$$

with the functional

$$\varphi(\lambda) = \frac{\displaystyle\int_\Omega \mathrm{e}^{q_\lambda(\xi)} \left[(w_\lambda(\xi), A_\lambda(\xi) w_\lambda(\xi)) - \hat{a}_\lambda(\bar{x}) \bar{x}_{\bar{\lambda}}^2(\xi) \right] \mathrm{d}\xi}{\displaystyle\int_\Omega \mathrm{e}^{q_\lambda(\xi)} \bar{x}_{\bar{\lambda}}^2(\xi)\, \mathrm{d}\xi} \tag{4.4}$$

where we have introduced the notation $w_\lambda(\xi) = \operatorname{grad} \bar{x}_{\bar{\lambda}}(\xi) + \bar{x}_{\bar{\lambda}}(\xi) \operatorname{grad} q_\lambda(\xi)$.

Remark 4.1. Replacing nonpercolation boundary condition (4.2) by the homogeneous Dirichlet conditions $x_\lambda(\xi, t) \equiv 0,\ \xi \in \partial\Omega$, corresponding to an absorbing boundary, we obtain the same result.

Remark 4.2. If we replace the functional by a monotone function of it, then the solution to the optimization problem remains the same.

Remark 4.3. Minimization problem (4.3) requires less smoothness of functions entering functional (4.4) than that for equation (4.1). It occurs in this case that the functions providing the minimal solutions possess the smoothness required for equations. Therefore, in practical calculations we may approximate only those derivatives that participate in functional (4.4).

In essence, expression (4.4) is the spatial energy functional of the corresponding stationary boundary value problem adapted for translations along the gradient of the potential $q_\lambda(\xi)$. For a fixed value of λ it attains the minimal value $\varphi_{\min}(\lambda)$ on the eigenfunctions $\bar{x}_\lambda(\xi)$ corresponding to the maximal eigenvalue of the differential operator from the right-hand side of system (4.1) self adjoint in the norm determined by the denominator of expression (4.4). The comparison of variational properties (see, e.g., [11]) of such functions with the corresponding properties of actually observed distributions allows us to make the conclusion that the process of spatial succession is completed in the community. For example, the presence of spatial ‘ripple’ observed without any external cause and having sufficiently regular periodic structure indicates that the community must go a long way to its evolutionary final.

The use of the methods described in this section allows us to justify the construction of the models of phenomena forming the base of the correlation adaptometry widely used in medical and biological practice (see [21]). Paper [22] contains a brief description of the model and application of the method to one of problems related to estimation of obesity treatment efficiency.

5. Models with continuous spatial-age structure

In the case when we have to take into account both the age and spatial population distributions considered above, we can construct conditions [20] for which there exists a sufficiently simple functional taking extremal values for the species consolidated in the course of evolution.

Constructing the model below, we use notations from previous sections whenever possible. Let $x_\lambda = x_\lambda(a,\xi,t)$ denote the spatial-age distribution density of the species with the number $\lambda \in \Lambda$, $h_\lambda x_\lambda = \operatorname{div}(D_\lambda(\xi)\,\operatorname{grad} x_\lambda)$, where $D_\lambda(\xi) > D_\lambda > 0$ is the operator of diffusion in spatial variables. Further, let $x = \{x_\lambda\}$, $\lambda \in \Lambda$ be the vector of current distributions, $m_\lambda = m_\lambda^\xi(\xi,x) + m_\lambda^a(a,x)$ be the mortality rates split into spatial dependent and age dependent ones, $\partial = \partial_t + \partial_a$. The model of the process of evolutionary selection is implemented under the indicated conditions in the following system of equations:

$$\partial x_\lambda = (h_\lambda - m_\lambda)x_\lambda, \quad \lambda \in \Lambda \tag{5.1}$$

with the conditions on the boundary of the age interval

$$x_\lambda(0,\xi,t) = \int_0^\infty b_\lambda(a) x_\lambda(a,\xi,t)\,\mathrm{d}a \tag{5.2}$$

and the conditions on the boundary of the spatial domain

$$x_\lambda(a,\xi,t)\,|_{\xi\in\partial\Omega} = 0. \tag{5.3}$$

From the viewpoint of possible biological interpretations, the hypotheses implemented in system (5.1)–(5.3) are quite acceptable, though they go back to the conditions specified by the general quasilinear theory ([18, 19]). For example, the assumption that the species-specific birth rate $b_\lambda(a)$ depends only on the age means a regularization of the reproduction process on the genetic level without any interference of population factors. For example, this hypothesis is confirmed for many species of protozoa. The hypothesis on splitting of the mortality rate appears to be considerably more discussion. However, from the viewpoint of conformity of this hypothesis to the practice of field studies, we should not forget that the most real data for theoretical consideration are connected to one-dimensional distributions in one way or another, which often poses a theoretical problem of constructing some functions associating simple one-dimensional observations to many-dimensional distributions more or less adequate to reality. Finally, boundary conditions (5.3) characterize the spatial domain as common for all considered species. Alternative nonpercolation conditions are also quite acceptable, so that the nature of the results does not differ from those described below.

Considering system (5.1)–(5.3), the main result of the theory is formulated in the following way. If the indicated system has a stable position of equilibrium $\bar{x}$, then the values $\bar{\lambda} \in \operatorname{supp}(\bar{x})$ are solutions to the optimization problem

$$\max_{\lambda\in\Lambda}\ \max_{w\in H_0^1(\Omega)} \varphi(\lambda,\bar{x},w)$$

with the functional

$$\varphi(\lambda,\bar{x},w)=\int_0^\infty b_\lambda(a)\exp\left(-\varkappa a-M_\lambda(\bar{x},w)-\int_0^a m_\lambda^a(s,\bar{x})\,\mathrm{d}s\right)\mathrm{d}a$$

where

$$M_\lambda(\bar{x},w)=\frac{\displaystyle\int_\Omega\left[(D_\lambda(\xi)\,\mathrm{grad}\,w_\lambda(\xi),\mathrm{grad}\,w_\lambda(\xi))-m_\lambda^\xi(\xi,\bar{x})w_\lambda^2(\xi)\right]\mathrm{d}\xi}{\displaystyle\int_\Omega w_\lambda^2(\xi)\,\mathrm{d}\xi}.$$

Here $H_0^1(\Omega)$ is the set of functions continuously differentiable with respect to spatial variables and satisfying boundary condition (5.3). In this case the optimal stationary solution is split, i.e., $\bar{x}_{\bar{\lambda}}(a,\xi)=\bar{v}_{\bar{\lambda}}(a)\bar{w}_{\bar{\lambda}}(\xi)$ with the following partial profiles: the spatial one $\bar{w}_{\bar{\lambda}}(\xi)$ realizing the minimum of the functional $M_{\bar{\lambda}}(\bar{x},w)$ on the set $H_0^1(\Omega)$ equal to $-\varkappa_{\bar{\lambda}}$, and the age one $\bar{v}_{\bar{\lambda}}(a)$ being the solution to the boundary value problem

$$\begin{aligned}\partial_a v_{\bar{\lambda}}(a)&=\left(\varkappa_{\bar{\lambda}}-m_{\bar{\lambda}}^a(a,\bar{x})\right)v_{\bar{\lambda}}(a)\\ v_{\bar{\lambda}}(0)&=\int_0^\infty b_{\bar{\lambda}}(a)v_{\bar{\lambda}}(a)\,\mathrm{d}a.\end{aligned}$$

A particular example of application of the construction presented in this section was presented in [20] where the metabolism rate was used as the selection parameter.

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