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MODELLING FOOD PREFERENCES AND VIABILITY CONSTRAINTS

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ABSTRACT

Differential inclusions arising in population biology are analysed and a numerical approach to solve the corresponding initial value problems is proposed. These differential inclusions originate from optimal myopic strategies and from projecting differential equations onto a viability set. We show that such differential inclusions may piecewise be considered either as ordinary differential equations or as differential-algebraic equations with Index 2. The numerical method is based on this observation. Simulations for one population of predators feeding on two populations of prey and for a system of two competing populations whose growth is constrained by a limited resource are given.

Keywords: Differential inclusions, population dynamics, control systems, numerical methods.

1. Introduction

Two new approaches to construct models of interacting populations were recently proposed, see [4] and [10]. Both of them lead in the last analysis to differential inclusions rather than to differential equations. In [4] complex food webs are modelled as control systems, where the controls may have various meanings, for example, they may model selective feeding for predators or selective escape for prey, etc. Since it is well known that predators exhibit feeding preferences, some internal strategies were considered. *Optimal myopic solutions* were defined to be the solutions of the control system that are driven by a particular strategy that is locally optimal. This approach was used to model cyclic behavior of the star-fish *Acanthaster planci* on Great Barrier Reef [1]. It was shown that feeding preferences of this star-fish may cause cyclic oscillations in its density.

Since biological systems must satisfy certain constraints, which may be given by the environment, it is natural to include these constraints into the description of the system. These constraints define the so called *viability set.* The only biologically plausible solutions are those that belong to the viability set at every instant of time. The viability theory solves the problem of the existence of viable solutions,

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see [2] and [3]. In [11] a method for correcting the dynamics at those points where no viable solution of the original system exists was developed. It consists in the "projection" of the dynamics onto the contingent cone to the viability set. This process typically leads to differential inclusions.

Difficulties arise if one wants to perform simulations of the above-mentioned problems. Since we are dealing with differential inclusions, the standard numerical procedures like Euler method or Runge-Kutta method may not give satisfactory results, compare [12]. For example, using an explicit Runge-Kutta method often leads to rapid oscillations. Therefore, more advanced numerical methods should be used. In case of optimal myopic strategies the approach given in [14] is applicable which is suited for the numerical treatment of differential inclusions arising from differential equations with discontinuous right-hand side of a special structure. In case when the solution is unique the methods analyzed in [8] and [9] can be applied.

In this paper we model simple dynamical systems including optimal myopic strategies and/or viability constraints. Under certain conditions and using the special structure of our problems we will show that the resulting differential inclusion can be restated piecewise either as an ordinary differential equation (ODE) or as a differential-algebraic equation (DAE) with Index 2. This observation allows to use suitable methods (depending on the structure of the right-hand side) for ODEs and DAEs to successively compute the solution on subintervals where the structure remains constant. This is a first step for treating biologically interesting examples numerically with methods of high precision.

2. Food Preferences and Viability Constraints

In [4] an approach for modelling food preferences and other possible strategies was developed. It was shown that "local" or "myopic" optimality may be described by the following control system

$$\begin{aligned} x'(t) &= a(x(t)) + B(x(t))u(t) && \text{for almost all } t \in [0,T], \\ u(t) &\in S(x(t)) && \text{for all } t \in [0,T], \\ x(t) &\in K && \text{for all } t \in [0,T] \end{aligned} \tag{2.1}$$

where $x \in \mathbf{R}^n$ is the vector of populations densities, $a : \mathbf{R}^n \to \mathbf{R}^n$, $B : \mathbf{R}^n \to Mat(n,l)$, ($Mat(n,l)$ denotes the set of all $n \times l$ matrices) are continuous maps. The set-valued map S is called *the strategy map* and associates to any x the set of possible controls from a given set $\mathcal{U}$ which locally maximize a given cost function. Thus for S the following form is assumed

$$S(x) = \left\{ u \in \mathcal{U} \,|\, d(x,u) = \max_{v \in \mathcal{U}} d(x,v) \right\} \tag{2.2}$$

where $\mathcal{U} \subset \mathbf{R}^l$, and

$$\mathcal{U} := \left\{ u \in \mathbf{R}^l \mid \sum_{j=1}^{l} u_j = 1,\ u_j \geq 0,\ j = 1, \ldots, l \right\}.$$

Let us note that it is also possible to consider the case when the map S is given by several functions d^i. The nonempty closed set K denotes the *viability set* which is given by p constraints, i.e.

$$K = \{x \in \mathbf{R}^n \mid r_1(x) \leq 0, \ldots, r_p(x) \leq 0\}. \tag{2.3}$$

For $x \in K$ we define the set of active constraints

$$I^1(x) := \{i = 1, \ldots, p \mid r_i(x) = 0\} \ .$$

In population biology a "natural" viability set K is the positive orthant but more complicated sets may easily be considered. Such sets may be given for example by constraints on the size of the "space" in which populations live. If we set

$$F(x) := \{a(x) + B(x)u \mid u \in S(x)\}, \tag{2.4}$$

(2.1) becomes a *constrained differential inclusion*

$$\begin{aligned} x'(t) &\in F(x(t)), \\ x(t) &\in K. \end{aligned} \tag{2.5}$$

There may exist no viable solution of (2.5), i.e. a solution which stays in K. Viability theory (see [2], [3]) gives necessary and sufficient conditions under which a viable solution exists. Besides some technical assumptions it is necessary that the feedback map

$$R(x) = F(x) \cap T_K(x) \tag{2.6}$$

has nonempty values in K. Here $T_K(x)$ stands for the *Bouligand contingent cone,* see [3]. In other words, the above tangential condition means that for each point on the boundary of the set K there exists at least one control $u \in S(x)$ for which $a(x) + B(x)u$ is "tangential" to the set K. In the case $R(x) = \emptyset$ for some $x \in K$ there is no viable solution starting from x. In order to achieve viability for the system the right-hand side of the differential inclusion must be changed at least at those points where $R(x) = \emptyset$. This can be done by projecting the right-hand side of the differential inclusion (2.5) onto the contingent cone to the set K. Such an approach which leads to a "projected differential inclusion" was used in [10]. In [11] it was shown that under some appropriate conditions the projected differential inclusion has the same solutions as the following inclusion

$$\begin{aligned} x'(t) &\in F(x(t)) - C_+(G(x(t))) \\ x(t) &\in K, \end{aligned} \tag{2.7}$$

where $G : K \rightsquigarrow \mathbf{R}^n$ is a given set-valued map and $C_+(G(x))$ denotes the positive cone spanned by $G(x)$. The meaning of the set $G(x)$ is to give directions along which the dynamics $F(x)$ can be projected, see Example 1 below for a reasonable choice of the map G. To give a numerical algorithm to solve the initial value problem corresponding to (2.7) we assume that the set-valued map $G(.)$ is given through m single valued maps $g_i : \mathbf{R}^n \to \mathbf{R}$, $i = 1, \ldots, m$. For every $x \in K$ we define

$$G(x) = \mathrm{conv}\{g_i(x) \mid i \in I^1(x)\} \ , \tag{2.8}$$

where conv denotes the convex hull. Moreover, we will assume that the cost function d is linear in controls, i. e.

$$d(x,u) = d^1(x)u_1 + \cdots + d^l(x)u_l.$$

For $i \in \{1, \ldots, l\}$ we define

$$R^i := \{x \in \mathbf{R}^n \mid d^i(x) > d^j(x) \ \text{ for every } \ j \neq i, \ j \in \{1, \ldots, l\}\} \ .$$

Then for every $x \in R^i$, $i \in \{1, \ldots, l\}$ the strategy map $S(x)$ is single valued and we denote its unique value by $u^i = (u_1^i, \ldots, u_l^i) \in \mathcal{U}$. Furthermore, we get

$$u_j^i = \begin{cases} 1 & \text{if } \ j = i \\ 0 & \text{otherwise.} \end{cases}$$

Define

$$I^2(x) := \left\{ i \in \{1, \ldots, l\} \mid d^i(x) = \max_{j \in \{1, \ldots, l\}} d^j(x) \right\} \ .$$

Let us note that for $x \in R^i$, $I^2(x)$ is single valued. Vectors $\{v_1, \ldots, v_k\}$, $v_i \in \mathbf{R}^n$ are called *geometrically independent* if $\{v_1 - v_k, \ldots, v_{k-1} - v_k\}$ are linearly independent. We will assume that if $I^2(x)$ contains at least two elements then

$$\{\nabla d^i(x) \mid i \in I^2(x)\} \quad \text{are geometrically independent} \ . \tag{2.9}$$

In this case the set $\mathbf{R}^n \setminus \bigcup_{i=1}^l R^i$ has zero Lebesgue measure in $\mathbf{R}^n$ and

$$I^2(x) = \{i \in \{1, \ldots, l\} \mid x \in \mathrm{cl}(R^i)\} \, .$$

Since the set $S(x)$ is a polyhedral set with extremal points u^i, $i \in I^2(x)$ we get

$$S(x) = \left\{ u \in \mathbf{R}^l \mid u = \sum_{i \in I^2(x)} \mu_i u^i, \ \sum_{i \in I^2(x)} \mu_i = 1, \ \mu_i \geq 0, \ i \in I^2(x) \right\} \ .$$

Hence, the differential inclusion (2.7) can equivalently be written as

$$\begin{aligned} x'(t) &= a(x(t)) + B(x(t)) \sum_{i\in I^2(x(t))} \mu_i(t)u^i(t) - k(t) \sum_{i\in I^1(x(t))} \lambda_i(t)\, g_i(x(t)) \;, \\ 1 &= \sum_{i\in I^2(x(t))} \mu_i(t), \quad \mu_i(t) \geq 0, \quad i \in I^2(x(t)) \;, \\ k(t) &\geq 0, \\ 1 &= \sum_{i\in I^1(x(t))} \lambda_i, \quad \lambda_i(t) \geq 0, \quad i \in I^1(x(t)) \;, \\ r_i(x(t)) &\leq 0, \quad 1 \leq i \leq p \;. \end{aligned} \tag{2.10}$$

Let us note that the existence theorem for (2.10) can be obtained from [11].

A solution $x : [0,T] \to \mathbf{R}^n$ of the initial value problem corresponding to (2.10) is called *piecewise active* if the index sets $I^1(x(t))$ and $I^2(x(t))$ are changing only at a finite number of points $\tau_l \in [0,T]$, $l = 1,\ldots,k$. We will assume that $x(\cdot)$ is piecewise active and consider an interval $[\tau_l, \tau_{l+1}]$ on which $I^1(x(t)) = I^1$ and $I^2(x(t)) = I^2$ hold for $t \in [\tau_l, \tau_{l+1}]$. Furthermore, we choose a fixed $i_0 \in I^2$. With help of i_0 we can eliminate $\mu_{i_0} = 1 - \sum_{i\in I^2, i\neq i_0} \mu_i$ from the system (2.10). If I^2 contains only one element we have $\mu_{i_0} = 1$. We define $v_i := k\,\lambda_i$. Note that $k = \sum_{j\in I^1} v_j$, $\lambda_j = v_j/k$. Hence, we can recompute k, λ_j from v_j if $k \neq 0$. The case $k = 0$ is of no practical importance because it means that no projection is necessary. Now, for every index $i \in I^2$, $i \neq i_0$

$$d^i(x(t)) - d^{i_0}(x(t)) = 0$$

has to be satisfied because of the definition of the strategy map. Then on $[\tau_l, \tau_{l+1}]$ we have to solve the following initial value problem for a *differential-algebraic equation*

$$\begin{aligned} y'(t) &= a(y(t)) + \sum_{i\in I^2, i\neq i_0} \mu_i(t) B(y(t))(u^i(t) - u^{i_0}(t)) \\ &\quad + B(y(t))u^{i_0}(t) - \sum_{j\in I^1} v_j(t) g_j(y(t)) \;, \\ 0 &= d^i(y(t)) - d^{i_0}(y(t)), \qquad i \in I^2,\ i \neq i_0 \;, \\ 0 &= r_j(y(t)), \qquad j \in I^1 \;, \\ y(\tau_l) &= x(\tau_l) \;. \end{aligned} \tag{2.11}$$

We refer to [6] and [13] for the treatment of differential algebraic equations (definition of index, existence and uniqueness of a solution, numerical treatment, etc.). In addition to the differential algebraic equation, the following inequalities have to be satisfied

$$0 \leq \mu_i(t) \leq 1, \qquad i \in I^2,\ i \neq i_0 \;, \quad v_j(t) \geq 0, \qquad j \in I^1$$

to ensure that the solution of the differential algebraic equation is a solution of the control problem we started with. Hence, we have additional conditions imposed on variables (of Index 2, cf. [6]) μ_i and v_j.

When solving (2.11) by a step-by-step numerical method one of the two index sets I^1 or I^2 may change between two steps. This change is necessary when one of the following *compatibility conditions* is violated

$$\begin{array}{ll}
\text{(a) } d^i(y(t)) - d^{i_0}(y(t)) < 0, & i \notin I^2,\ i \neq i_0 \ , \\
\text{(b) } r_j(y(t)) < 0, & j \notin I^1 \ , \\
\text{(c) } 0 \leq \mu_i(t) \leq 1, & i \in I^2,\ i \neq i_0 \ , \\
\text{(d) } v_j(t) > 0, & j \in I^1
\end{array}$$

at a certain discretization point. These conditions have to be checked after each computational step to ensure that the structure of (2.11) is chosen compatible to our original problem (2.5).

To achieve a higher order of convergence for a numerical method applied to the initial value problems corresponding to (2.5) it is essential to locate the points where a structural change occurs with high precision. In general, we have to combine an ODE/DAE-solver with modules for:

(i) Detecting a structural change (failure of compatibility conditions).
(ii) Locating the point where the structural change occurred.
(iii) Determining a new compatible structure.

After finishing steps (i)–(iii) we have to restart the ODE/DAE-solver at the localized point with the corresponding initial values and the new compatible structure.

Especially (iii) needs some further analysis. If one of the compatibility conditions is no longer valid we have to change the index sets. In case that (a) or (b) fails for some indices, we add these indices to the corresponding index set, and if (c) fails for some indices we remove those indices from I^2. If (d) is no longer true for some indices, these indices have to be removed from I^1. With the new index sets we compute the solution of the resulting ODE/DAE and test the compatibility conditions once more. In case (a) incompatibility of the newly determined structure may occur. In this case it is necessary to exchange i_0 and to remove some of the added indices from the index set I^2.

3. Simulations

As underlying numerical method for solving the arising initial value problems for the ODE's and DAE's with Index 2 we used the code RADAU5, see [6] and [7]. The points where the index is changing were localized by a bracketing method.

Example 1. [Two populations depending on one resource.] Let us consider two populations whose densities are denoted by x_1, x_2, which are constrained by "space" S. It is assumed that the growth of these two populations is described by a logistic equation, i.e.

$$x'_1(t) = x_1(t)(a_1 - b_1x_1(t)) ,$$
$$x'_2(t) = x_2(t)(a_2 - b_2x_2(t)) ,$$
$$x_1(t) + x_2(t) \le S(t) .$$

Choosing $G(x) := (x_1, x_2)$ gives the following form of (2.10)

$$x'_1(t) = x_1(t)(a_1 - b_1x_1(t)) - k(t)x_1(t) ,$$
$$x'_2(t) = x_2(t)(a_2 - b_2x_2(t)) - k(t)x_2(t) ,$$
$$k(t) \ge 0 ,$$
$$x_1(t) + x_2(t) \le S(t) .$$

For $x_1(t) + x_2(t) = S(t)$ the projected system has the form

$$x_1' = x_1(a_1 - b_1x_1 - \frac{x_1(a_1 - b_1x_1) + x_2(a_2 - b_2x_2) - S'}{S}),$$
$$x_2' = x_2(a_2 - b_2x_2 - \frac{x_1(a_1 - b_1x_1) + x_2(a_2 - b_2x_2) - S'}{S}) .$$

The solution of the initial value problem with initial values

$$x_1(0) = 0.5, \quad x_2(0) = 0.3,$$

parameters

$$a_1 = 1.0, \quad a_2 = 0.5, \quad b_1 = 1.0, \quad b_2 = 0.3,$$

and resource limiting function

$$S(t) = \exp(0.2(50.0 - t)) + 1$$

is plotted in Fig. 1. First, the system is not limited by the available space and reaches its equilibrium given by $(a_1/b_1, a_2/b_2)$. At a certain time t_1 when $S(t_1) = a_1/b_1 + a_2/b_2$, the constraint becomes active, the dynamics changes and the system reaches a new "environmentally induced" equilibrium.

Example 2. [Optimal myopic strategy.] In [4] a simple system of one population of predators feeding on two populations of prey was considered. The dynamics was described by Lotka–Volterra-like equations, with no self-saturation and competition between two populations of prey. Here we consider the same system, but we include self-saturation and competition for prey populations, i.e.

$$x'_1(t) = \alpha_1x_1(t) - \beta_{11}x_1(t)^2 - \beta_{12}x_1(t)x_2(t) - \kappa_1x_1(t)x_3(t)u_1(t) ,$$
$$x'_2(t) = \alpha_2x_2(t) - \beta_{21}x_1(t)x_2(t) - \beta_{22}x_2(t)^2 - \kappa_2x_2(t)x_3(t)u_2(t) ,$$
$$x'_3(t) = x_1(t)x_3(t)u_1(t) + x_2(t)x_3(t)u_2(t) - \gamma_3x_3(t) ,$$

with $u_1(t),\ u_2(t) \ge 0,\ u_1(t) + u_2(t) = 1$ and $x_1(t),\ x_2(t)$ the densities of the prey and $x_3(t)$ the density of the predator at the time t. We assume, that the control of feeding is chosen such that

$$d(x, u) = a\,u_1\,x_1 + b\,u_2\,x_2 = u_1(ax_1 - bx_2) + bx_2$$

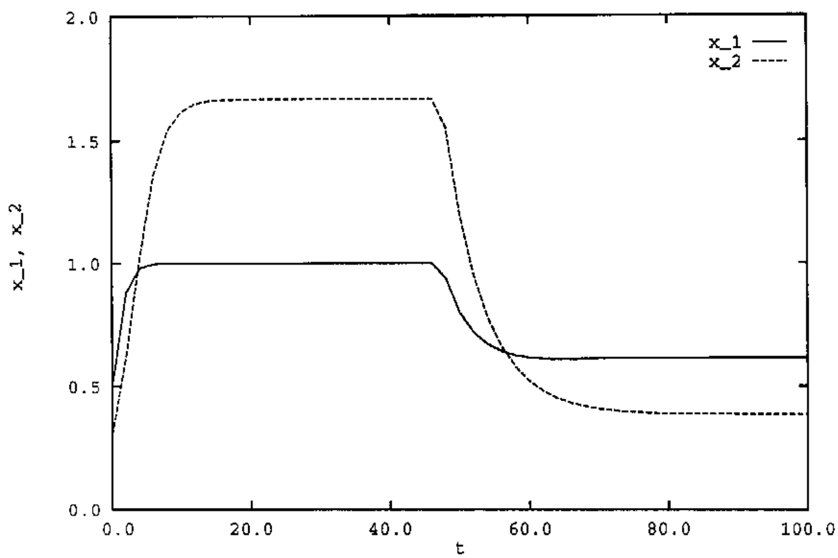

Fig. 1. Solution of Example 1.

is maximized at every instant of time. For $a = b = 1$ this can be interpreted as maximizing the relative growth rate, the case considered in [4].

Depending on the sign of $g(x) := a\,x_1 - b\,x_2$ we have to distinguish three cases

$$\begin{array}{ll} u_1 = 1 & \text{for } x \in G^+ := \{x \in \mathbf{R}^3 \mid g(x) < 0\}\,, \\ u_1 \in [0,1] & \text{for } x \in G^0 := \{x \in \mathbf{R}^3 \mid g(x) = 0\}\,, \\ u_1 = 0 & \text{for } x \in G^- := \{x \in \mathbf{R}^3 \mid g(x) < 0\}\,. \end{array}$$

The existence of a solution for the initial value problem for the resulting differential inclusion follows from [4]. For the above system it can also be proved that the solution is unique. Let us denote

$$f_n^+(x) := \langle n(x), f(x,1)\rangle, \;\; f_n^-(x) := \langle n(x), f(x,0)\rangle,$$

where $n(x) = (a, -b, 0)$ denotes the normal to G^0 oriented from G^- to G^+. For $x \in G_0$ fixed we may distinguish two cases

$$f_n^+(x) < 0\;, \quad f_n^+(x) \geq 0\;.$$

In case $f_n^+(x) \geq 0$ we use $f_n^-(x) = f_n^+(x) + a\kappa_1 x_1 x_3 + b\kappa_2 x_2 x_3$ to verify that in this case $f_n^-(x) > 0$ holds. Hence for every $x \in \mathbf{R}_+^n$ either $f_n^+(x) < 0$ or $f_n^-(x) > 0$ holds and we can apply Theorem 2, p. 111 in [5] to get uniqueness of the solution to the corresponding initial value problem. Uniqueness is important for the convergence of the proposed numerical method.

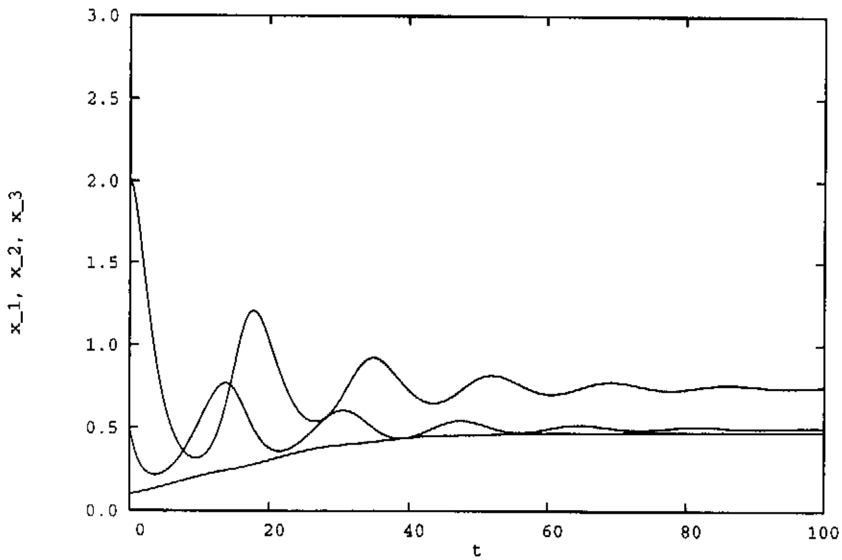

Fig. 2. Solution of Example 2 ($\beta_{11} = 0.2$).

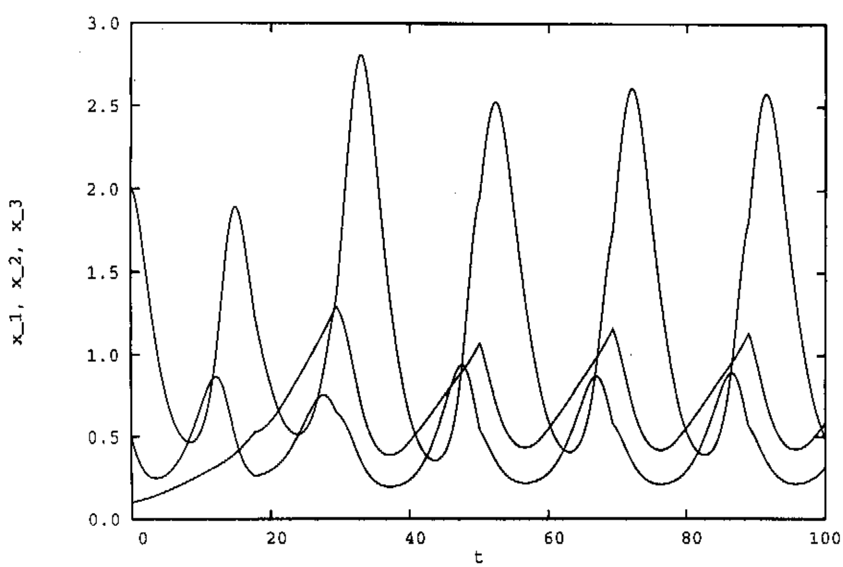

Fig. 3. Solution of Example 2 ($\beta_{11} = 0.01$).

For the numerical tests we used

$$\alpha_1 = 0.12,\ \alpha_2 = 0.4,\ \kappa_1 = 0.31,\ \kappa_2 = 0.37,\ \gamma_3 = 0.5a = 1.0,\ b = 2.0\,.$$

The remaining parameters are chosen as $\beta_{12} = \beta_{21} = 0.05$ and $\beta_{22} = \beta_{11}$ where β_{11} serves as a bifurcation parameter. Figures 2 and 3 show the asymptotic behaviour of a particular solution starting from the initial densities

$$x_1(0) = 0.1,\ x_2(0) = 0.5,\ x_3(0) = 2.0\,.$$

It can be seen that when the parameter β_{11} decreases under certain value, a cycle arises. This resembles Hopf bifurcation, but the mechanism behind it is different, since we are dealing with differential inclusion rather than with differential equation. Starting with different initial values indicates that the limit "cycle" is asymptotically stable.

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