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Construction of population growth equations in the presence of viability constraints

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Abstract. A mathematical method based on the G-projection of differential inclusions is used to construct dynamical models of population biology. We suppose that the system under study, not being limited by resources, may be described by a control system

$$\dot{x}(t) = f(x(t), u(t)),$$

where u is a control describing the choice of resources. Then considering the constraints that the system must satisfy we define a viability set K. Since there may not exist a control $u(\cdot)$ such that the corresponding solution satisfies $x(t) \in K$, we have to change the dynamics of the control system to get a viable solution. Using the G-projection we introduce so-called "projected" control system

$$\dot{x}(t) = \Pi^G_{T_K} f(x(t), u(t))$$

that has a viable solution. The projected system has usually simpler dynamics than traditional models used in population biology.

Key words: Population growth equations – Control systems – Differential equations – Viability theory – Projected differential inclusions

1. Introduction

Models based on differential equations have been used in population biology since the times of Lotka and Volterra. The state variables are usually the densities of the populations and/or resources and therefore they must satisfy certain constraints. For example, they must be non-negative. The general approach to model a system is to construct a differential equation in such a way that the solution satisfies all these constraints. Since in general linear models do not satisfy these constraints, non-linear models have been considered.

In this paper we show another possible approach. In general, biological systems have an endogeneous growth rate when they are provided with the resources they need. For example we can assume that without limitation by resources (nutrients, space, light etc.) a population will grow exponentially. If it does not, the reason is that it consumes scarce resources. The question is: How can we modify a dynamical system to make it viable (i.e. having solutions which do satisfy the constraints), knowing the dynamical behavior of the system without the state constraints. This already defined dynamics will be called endogeneous. Such endogeneous dynamics may be for example linear. Considering the constraints that the system must satisfy we define so called viability set. In many cases K is the positive orthant of the Euclidian space. Of course, the endogeneous dynamics may not have a viable solution, i.e. a solution satisfying the constraints. To get a viable solution we change the endogeneous dynamics using so-called G-projection. Since a population can choose among several resources we assume that the endogeneous dynamics can be described by a control system

$$\dot{x}(t) = f(x(t), u(t)), \qquad u(t) \in \mathcal{U}, \tag{1}$$

where $\mathcal{U}$ is a set of possible controls u that describe the selection of the resources. Let K denote the viability set. The viable solutions of (1) are those which obey

$$x(t) \in K \quad \text{for all } t \in [0, T]. \tag{2}$$

The system can obey Eq. (1) until it reaches the boundary of the viability set K. Then some constraints are active and if there is no control $u(\cdot) \in \mathcal{U}$ that keeps the system (1) in K the dynamics of (1) must change to keep the system viable. To make (1) viable it is enough to project the dynamics (1) onto the contingent cone to the set K [1]. Projected differential equations have been used to build planning models in economics by projecting the dynamics onto the tangent cone to the viability set defined by state constraints [3, 5]. Projection of the best approximation was used. Since this projection is not general enough to provide plausible models of population biology we use more general G-projection [6]. To define the G-projection we assume that a map G (in general set-valued) is given. The map gives directions in which (1) is projected. From a biological point of view to project (1) it means to increase the mortality rates of those populations that are limited by the lack of resources. It was proved [6] that the projected system has the same solutions as the following differential inclusion

$$\dot{x}(t) \in f(x(t), u(t)) - mG(x(t), u(t)), \qquad u \in \mathcal{U} \tag{3}$$

where the control parameter $m \geqslant 0$ can be interpreted as induced mortality rate that keeps the system viable.

The theory of the G-projected differential inclusions will be used to provide differential equations which are good candidates to model the evolution of the systems of population dynamics.

2. Endogeneous dynamics

In biology, chemistry, economics etc. it is quite usual to describe a system by an energy (or nutrient, money etc.) graph. Such a graph describes the flow of energy etc. between different parts of the system. In ecology such charts are also called food webs (or trophic nets) and we will use them to describe ecosystems. The components of such a graph will be different populations and/or abiotic resources.

Let us assume that a system of n populations and/or abiotic resources is given and let us construct a dynamic model of this system.

Since usually a population can use alternative resources we have to include in our model some controls that will allow to choose these resources according to the decision taken by the population. We introduce a class of matrices $\mathcal{U}$ that we will call "food web matrices". This class of matrices consists of all square matrices of dimension n for which the following holds:

$$u \in \mathcal{U} \quad \text{if and only if}$$

(i) $u_{ij} \geqslant 0$ if the j-th population can utilize the i-th component
(ii) $u_{ij} = 0$ otherwise
(iii) $\sum_{i=1}^{n} u_{ij} = 1$ if the j-th component of the graph is a population.

The value u_{ij} can be interpreted as the probability that the j-th population exploits the i-th component of the graph.

We assume that the endogeneous dynamics is described by the following control system

$$\dot{x}(t) = f(x(t), u(t)), \qquad u(t) \in \mathcal{U}. \tag{4}$$

We derive one reasonable form of the endogeneous dynamics (4). Let $A(x) \in Mat(n, n)$ be a matrix of the growth rates, where $a_{ij}(x)$ is the growth rate of the j-th population, if the resource of this population is the i-th component of the given system (such a component may be either another population or an abiotic resource). The simplest case is to take $a_{ij}(x)$ constant.

Let us construct differential equations describing the evolution of a system:

$$x_i(t + \Delta t) - x_i(t) = \left(z_i(t) + x_i(t) \sum_{j=1}^{n} a_{ji} u_{ji}(t) - \sum_{j=1}^{n} a_{ij} \alpha_{ij} u_{ij}(t) x_j(t) - n_i x_i(t) \right) \Delta t,$$
$$u(t) \in \mathcal{U},$$

i.e.

$$\dot{x}_i(t) = z_i(t) + x_i(t) \sum_{j=1}^{n} a_{ji} u_{ji}(t) - \sum_{j=1}^{n} a_{ij} u_{ij}(t) x_j(t) - n_i x_i(t), \qquad u(t) \in \mathcal{U}. \tag{5}$$

Here the functions z_i describe the growth of the abiotic resources, n_i are intrinsic mortality rates that do not depend on the resources and $\alpha_{ij} \geqslant 0$, $i, j = 1, \ldots, n$ are given transformation coefficients.

Example. In Fig. 1 we see a graph, describing the interactions of seven different populations $(x_2, \ldots, x_8)$ and an abiotic resource x_1.

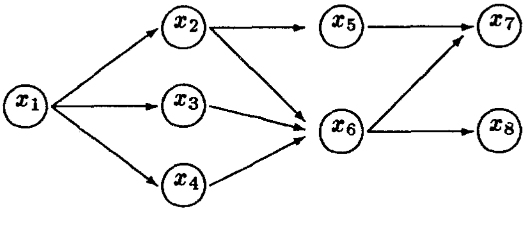

Fig. 1. A food web

For this system the food web matrices $u \in \mathcal{U}$ have the following form

$$u = \begin{pmatrix} 0 & 1 & 1 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & u_{26} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & u_{36} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & u_{46} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & u_{57} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & u_{67} & 1 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \end{pmatrix}, \tag{6}$$

$$u_{26} + u_{36} + u_{46} = 1, \qquad u_{57} + u_{67} = 1.$$

If we take the matrix of the growth rates A constant then (5) reads

$$\begin{aligned}
\dot{x}_1(t) &= z_1(t) - a_{12}\alpha_{12}x_2(t) - a_{13}\alpha_{13}x_3(t) - a_{14}\alpha_{14}x_4(t) \\
\dot{x}_2(t) &= a_{12}x_2(t) - a_{25}\alpha_{25}x_5(t) - a_{26}\alpha_{26}u_{26}(t)x_6(t) - n_2x_2(t) \\
\dot{x}_3(t) &= a_{13}x_3(t) - a_{36}\alpha_{36}u_{36}(t)x_6(t) - n_3x_3(t) \\
\dot{x}_4(t) &= a_{14}x_4(t) - a_{46}\alpha_{46}u_{46}(t)x_6(t) - n_4x_4(t) \\
\dot{x}_5(t) &= a_{25}x_5(t) - a_{57}\alpha_{57}u_{57}(t)x_7(t) - n_5x_5(t) \\
\dot{x}_6(t) &= x_6(t)(a_{26}u_{26}(t) + a_{36}u_{36}(t) + a_{46}u_{46}(t)) - a_{67}\alpha_{67}u_{67}(t)x_7(t) \\
&\quad - a_{68}\alpha_{68}x_8(t) - n_6x_6(t) \\
\dot{x}_7(t) &= x_7(t)(a_{57}u_{57}(t) + a_{67}u_{67}(t)) - n_7x_7(t) \\
\dot{x}_8(t) &= x_8(t)a_{68} - n_8x_8(t).
\end{aligned}$$

3. Viability constraints

Let us assume there are some "viability constraints" that the system must satisfy. We assume that these constraints are given by p functions $r_i(\cdot)$, $i = 1, \ldots, p$ and we define the viability set K

$$K := \{x \in \boldsymbol{R}^n \mid r_1(x) \leqslant 0, \ldots, r_p(x) \leqslant 0\}. \tag{7}$$

For biological reasons we may assume that the set K is bounded. Moreover, we assume that $r_i(\cdot)$ are Fréchet differentiable and the following transversality condition is satisfied for all $x \in K$

$$\exists v_0 \in \boldsymbol{R}^n \text{ such that } \langle r_i'(x), v_0 \rangle < 0 \text{ if } r_i(x) = 0. \tag{8}$$

Here $\langle ., . \rangle$ stands for the scalar product in $\boldsymbol{R}^n$. Let $x \in K$,

$$T^i(x) := \{v \in \boldsymbol{R}^n \mid \langle r_i'(x), v \rangle \leqslant 0 \text{ if } r_i(x) = 0\}. \tag{9}$$

Let

$$T_K(x) := \left\{ v \in \boldsymbol{R}^n \,\middle|\, \liminf_{h \to 0_+} \frac{d_K(x + hv)}{h} = 0 \right\}$$

($d_K(x)$ denotes the distance of x from the set K) denotes the contingent cone to the set K at x [1, 2]. Then

$$T_K(x) = \bigcap_{i=1}^{n} T^i(x)$$

[2].

In population biology typical case is $p = n$, where n is the dimension of the system and $r_i(x) = -x_i$, i.e.

$$K := \{x \in \boldsymbol{R}^n \mid x_1 \geqslant 0, \ldots, x_n \geqslant 0\}. \tag{10}$$

4. Projected system

In general, the control system (4) may not have a viable solution, i.e. there may not exist a control $u(t) \in \mathcal{U}$ such that the corresponding trajectory satisfies the viability constraints

$$x(t) \in K, \qquad t \in [0, T], \quad T > 0.$$

It means there is no policy for the populations to choose resources (through u_{ij}) in such a way that the system will stay in the set K. If we define the feedback map $R(\cdot)$

$$R(x) := \{u \in \mathcal{U} \mid f(x, u) \in T_K(x)\},$$

then it means

$$\exists x \in K, \qquad R(x) = \varnothing, \tag{11}$$

see [1, 4]. Since the feedback map $R(\cdot)$ contains all the controls $u \in \mathcal{U}$ that keep the corresponding solutions to (4) in the set K, (11) means there does not exist an "internal control" (in our interpretation this control means food selection) that could provide a viable trajectory. Therefore the mortality rate of those populations that are limited by the lack of resources must increase. This can occur only on the boundary of the viability set K (in the interior of the set K is $T_K(x) = \boldsymbol{R}^n$ and consequently $R(x) \neq \varnothing$). Introducing mortality induced by the scarcity of resources, the system (4) has the following form

$$\dot{x}(t) \in f(x(t), u(t)) - mG(x(t), u(t)), \qquad u(t) \in \mathcal{U}, \quad \begin{matrix} m > 0 & \text{if } R(x(t)) = \varnothing \\ m = 0 & \text{if } R(x(t)) \neq \varnothing \end{matrix} \tag{12}$$

where the map $G(\cdot\,, \cdot)$ (in general set-valued) must be specified and m is regarded as a control parameter (induced mortality rate) that keeps the system viable.

The differential inclusion (12) can be also written in the following equivalent form

$$\dot{x}(t) \in f(x(t), u(t)) - C_+(G(x(t), u(t))), \tag{13}$$

where $C_+(G(x, u))$ denotes the positive cone spanned by $G(x, u)$, see Definition 1A.

It was proved (see Theorems 1A and 2A) that under certain conditions there exists a solution to (13) and, moreover, (13) has the same solution set as the following G-projected control system (1) (for definition of G-projection see Definition 2A):

$$\dot{x}(t) \in \Pi^G_{T_K}(f(x(t), u(t))) := \Pi^{G(x(t),u(t))}_{T_{K(x(t))}}(f(x(t), u(t))), \qquad u(t) \in \mathcal{U}. \tag{14}$$

First we need to define the set-valued map $G(\cdot\,,\cdot)$,

$$G:\Omega \times \mathscr{U} \rightsquigarrow \boldsymbol{R}^n,$$

where

$$\Omega := \{x \in K \mid f(x, u) \notin T_K(x), \forall u \in \mathscr{U}\}. \tag{15}$$

Let

$$\Omega := \{x \in K \mid r_i(x) = 0\},$$

and

$$I(f(x, u)) := \{i = 1, \dots, p \mid r_i(x) = 0, \langle r_i'(x), f(x, u)\rangle > 0\},$$

denote the subset of active constraints.

Let $g_i : \Omega_i \times \mathscr{U} \to \boldsymbol{R}^n$ be given functions. Then we define

$$G(x, u) := \operatorname{conv}\{g_i(x, u) \mid i \in I(f(x, u))\}. \tag{16}$$

Here conv stands for the convex hull.

If the viability set is defined by (10) then for $\forall(x, u) \in \Omega_i \times \mathscr{U}$ we define

$$g_i(x, u) := (u_{i1}\alpha_{i1}x_1, \dots, u_{in}\alpha_{in}x_n) - \left(\sum_{j=1}^{n} u_{ij}\alpha_{ij}x_j\right)e_i, \tag{17}$$

where $e_i \in \boldsymbol{R}^n$, $e_{ij} = 0$ for $i \neq j$ and $e_{ii} = 1$. The biological meaning of this choice reflects two assumptions:

(1) We change the growth rate only of those populations whose growth is limited by the lack of resources.
(2) The induced mortality for each population is at least a linear function of its density.

From the computational point of view it is quite unpleasant that since $G(\cdot\,,\cdot)$ is a set-valued map, the right hand side of (14) is set-valued too. Let us define for all $x \in K$, $u \in \mathscr{U}$

$$\pi(f(x, u)) :=$$

$$\begin{cases} \{f(x, u) - kg \mid g \in G(x, u), k \geqslant 0, \langle r_i'(x), f(x, u) - kg\rangle = 0, & \\ \forall i \in I(f(x, u))\} & \text{if } x \in \Omega \\ f(x, u) & \text{otherwise.} \end{cases} \tag{18}$$

In Theorem A3 we give some conditions under which $\pi(\cdot\,,\cdot)$ is single valued selection from $\Pi^G_{T_K}$. Moreover, we prove that the following control system

$$\dot{x}(t) = \pi(x(t), u(t)), \qquad u(t) \in \mathscr{U} \tag{19}$$

has the same solutions as (14).

5. A description of competing populations

Let x_1 denote the resource for which n populations $x_2, \dots, x_{n+1}$ compete. Let us suppose that the growth of each population without limitation can be described by the following differential equation:

$$\dot{x}_i(t) = a_i x_i(t) - n_i x_i(t), \qquad i = 2, \dots, n+1, \tag{20}$$

with $a_i > n_i > 0$, $i = 2, \dots, n+1$.

As concerns the resource we distinguish two possibilities:
(1) the resource is nondestructible (for example space);
(2) the resource (for example nutrient) is used up by the populations.

(1) The first case gives the following equation for the "free" space

$$\dot{x}_1(t) = -\sum_{i=2}^{n+1} \alpha_i (a_i x_i - n_i x_i), \tag{21}$$

where $\alpha_i > 0$, $i = 2, \ldots, n+1$ denote the transformation coefficients.

Let

$$K := \{x \in \boldsymbol{R}^{n+1} \mid x_i \geqslant 0, i = 1, \ldots, n+1\} \cap B(0, d),$$

where $B(0, d)$ is a ball with radius d. The reason why we use $B(0, d)$ is just to have the set K bounded. Let

$$\Omega := \left\{ x \in K \,\middle|\, \left(q - \sum_{i=2}^{n+1} \alpha_i (a_i x_i - n_i x_i), (a_1 - n_1) x_1, \ldots, (a_{n+1} - n_{n+1}) x_{n+1} \right) \notin T_K(x) \right\}.$$

It is easy to see that (20), (21), does not have a non-trivial viable solution in the set K. Since

$$T_K(x) = \{v \in \boldsymbol{R}^n \mid v_i \geqslant 0 \text{ if } x_i = 0\},$$

it follows that the only active constraint is $x_1 = 0$.

Let us project (20), (21) onto the contingent cone using G defined by (16), i.e.

$$G(x) = g_1(x) := \left(-\sum_{i=2}^{n+1} \alpha_i x_i, \alpha_2 x_2, \ldots, \alpha_{n+1} x_{n+1} \right), \quad \forall x \in \Omega_1 = \{x \in K \mid x_1 = 0\}.$$

We may calculate explicitly the projected system (14). If $x_1(t) > 0$ then

$$\dot{x}_1(t) = -\sum_{i=2}^{n+1} \alpha_i (a_i x_i(t) - n_i x_i(t))$$

$$\dot{x}_i(t) = a_i x_i(t) - n_i x_i(t), \qquad i = 2, \ldots, n+1.$$

If $x_1(t) = 0$ then

$$\dot{x}_1(t) = 0$$

$$\dot{x}_i(t) = a_i x_i(t) - n_i x_i(t) - x_i(t) \frac{\sum_{j=2}^{n+1} \alpha_j (a_j x_j(t) - n_j x_j(t))}{\sum_{j=2}^{n+1} \alpha_j x_j(t)}. \tag{22}$$

(2) In the second case we assume that the resource is supplied with the rate $z(t)$, i.e.

$$\dot{x}_1(t) = z(t) - \sum_{i=2}^{n+1} \alpha_i a_i x_i(t). \tag{23}$$

The projected system has the following form

If $x_1(t) > 0$ then

$$\dot{x}_1(t) = z(t) - \sum_{i=2}^{n+1} \alpha_i a_i x_i(t)$$

$$\dot{x}_i(t) = a_i x_i(t) - n_i x_i(t), \qquad i = 2, \ldots, n+1. \tag{24}$$

If $x_1(t) = 0$ then

$$\dot{x}_1(t) = 0$$

$$\dot{x}_i(t) = a_i x_i(t) - n_i x_i(t) - x_i(t) \frac{\sum_{j=2}^{n+1} a_j \alpha_j x_j(t)}{\sum_{j=2}^{n+1} \alpha_j x_j(t)}, \qquad i = 2, \ldots, n+1.$$

The existence of a solution to these discontinuous differential equations follows from Theorem 1A and Theorem 2A.

6. Discussion

In this paper we used the method of G-projection of a control system onto a viability set to construct models of interacting populations. In fact, the G-projection can be seen as a method that "couples" possibly independent differential equations in such a way that the resulting equations satisfy given constraints. Since in many cases the dynamics of the system inside the set K is quite simple (for example linear) the resulting projected equation has simpler dynamics than the standard models of population biology. The price that we have to pay is that the right hand side of the projected system is not a continuous function. Therefore the existence results for the projected system are more complicated than in the continuous case.

Appendix

Here we recall some basic facts concerning the viability theory and G-projection of differential inclusions. More details can be found in [1, 2, 4, 6].

Definition 1A. Let $A \subset \boldsymbol{R}^n$. By $C_+(A)$ we denote the positive cone spanned by A, i.e.

$$C_+(A) := \begin{cases} \bigcup_{k \geqslant 0} kA & \text{if } A \neq \emptyset \\ \{0\} & \text{if } A = \emptyset. \end{cases}$$

Remark. Let $g \in \boldsymbol{R}^n$. Then instead of writing $C_+(\{g\})$ we will write $C_+(g)$.

Definition 2A. Let $K, M, G \subset \boldsymbol{R}^n$ be non-empty sets. Then

1. For every $g \in G$ and every $u \in M \cap (C_+(g) + K)$ define

$$k_g^K(u) := \inf\{k \geqslant 0 \mid u - kg \in K\},$$

$$\Pi_K^g(u) := u - k_g^K(u)g.$$

2. Let $M \cap (C_+(G) + K) \neq \emptyset$. Then

$$\Pi_K^G(M) := \bigcup_{g \in G} \bigcup_{u \in M \cap (C_+(g) + K)} \Pi_K^g(u).$$

We say that $\Pi_K^G(M)$ is the G-projection of the set M onto the set K.

Theorem 1A. *Let $K \subset X$ be a non-empty compact set, $\mathscr{U} \subset \boldsymbol{R}^{n \times n}$ be a compact set, $f: K \times \mathscr{U} \mapsto X$ be a continuous map. Let $\Omega \subset K$ be defined by* (15), *$G: \Omega \times \mathscr{U} \rightsquigarrow X$ be a set-valued map with non-empty convex compact values defined by* (16). *Let $C_+(G(\cdot\,,\cdot))$ have closed graph. Let*

$$\forall (x, u) \in K \times \mathscr{U}, \qquad f(x, u) \in T_K(x) + C_+(G(x, u)) \tag{25}$$

and

$$\sup_{(x,u) \in K \times \mathscr{U}} \inf_{g \in G(x,u)} \|f(x, u) - \Pi^g_{T_{K(x)}}(f(x, u))\| = c < \infty. \tag{26}$$

Moreover, let the set-valued map $M: K \rightsquigarrow X$,

$$M(x) := \{f(x, u) - (\bar{B}(0, c) \cap C_+(G(x, u))) \mid u \in \mathscr{U}\}$$

have closed convex values. Then for every $T > 0$ there exists a solution to (13).

Theorem 2A. *Let $K \subset X$ defined by* (7) *be a non-empty convex set, $\mathscr{U} \subset R^{n+n}, f: K \times \mathscr{U} \mapsto K$ be a single-valued map. Let $\Omega \subset K, G: \Omega \times \mathscr{U} \rightsquigarrow X$ be defined by* (15), (16). *Let $G(\cdot\,,\cdot)$ has non-empty convex values. Let for every $(x, u) \in \Omega \times \mathscr{U}$,*

$$G(x, u) \cap T_K(x) = \emptyset. \tag{27}$$

Then the solutions to (14) *are the viable solutions to* (13) *and conversely.*

In the next theorem we give some conditions under which (19) is a differential equation and has the same solution set as (13) and conversely.

Theorem 3A. *Let $K \subset \boldsymbol{R}^n$ defined by* (7) *be a non-empty set, $\Omega \subset \boldsymbol{R}^n$ be defined by* (15). *Let $f: K \rightsquigarrow \boldsymbol{R}^n$ be a continuous map, $G: \Omega \rightsquigarrow \boldsymbol{R}^n$ be set-valued map defined by* (16). *Let $T^i(\cdot)$ be defined by* (9) *and*

(*i*) $\quad \forall (x, u) \in K \times \mathscr{U}; \qquad f(x, u) \in T_K(x) + C_+(G(x, u)),$

(*ii*) $\quad \forall (x, u) \in \Omega \times \mathscr{U}; \qquad (C_+(G(x, u)) - C_+(G(x, u)))$

$$\cap \bigcap_{i \in I(f(x,u))} T^i(x) \cap \left(- \bigcap_{i \in I(f(x,u))} T^i(x) \right) = \{0\}.$$

Then $\pi(x, u)$ defined by (18) *is a single-valued selection from $\Pi^G_{T_K}(f(x, u))$ and the solutions to the differential equation* (19) *are the viable solutions to the differential inclusion* (13) *and conversely.*

For the proofs and more details we refer to [6].

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