

Computational methods for analyzing bistability in biochemical reaction networks

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Abstract—Bistability plays a key role in important biological processes, such as cell division, differentiation, and apoptosis. Examples show that there is a very delicate relationship between the structure of a reaction network and its capacity for bistable behavior. We describe mathematical methods that discriminate between networks that have the capacity for bistability and those that do not, as well as algorithms derived from these methods. We have implemented some of these algorithms in the software package BioNetX. We present results obtained by using this package to analyze random samples from a comprehensive database of reaction networks.

I. INTRODUCTION

A chemical reaction network is usually given by a finite list of reactions that involve a finite set of chemical species. As an example, consider the reaction network with two species A_1 and A_2 schematically given in the diagram (1).



To keep track of the temporal variation of the state of this chemical system, we define the functions $c_{A_1}(t)$ and $c_{A_2}(t)$ to be the molar concentrations of the species A_1, A_2 at time t . The chemical reactions in the network are responsible for changes in the concentrations; for instance, whenever the reaction $A_1 + A_2 \rightarrow 2A_1$ occurs, there is a net gain of a molecule of A_1 , whereas one molecule of A_2 is lost. Similarly, the reaction $2A_2 \rightarrow 2A_1$ results in the creation of two molecules of A_1 and the loss of two molecules of A_2 .

We will assume that the rate of change of the concentration of each species is governed by *mass-action kinetics* [12], i.e., that each reaction takes place at a rate that is proportional to the product of the concentrations of the species being consumed in that reaction. For example, under the mass-action kinetics assumption, the contribution of the reaction $A_1 + A_2 \rightarrow 2A_1$ to the rate of change of c_{A_1} has the form $k_{A_1+A_2 \rightarrow 2A_1} c_{A_1} c_{A_2}$, where $k_{A_1+A_2 \rightarrow 2A_1}$ is a positive number called *reaction rate constant*. Collecting these contributions from all the reactions, we obtain the following system of differential equations:

$$\begin{aligned} \dot{c}_{A_1} &= -k_{2A_1 \rightarrow A_1+A_2} \bar{c}_{A_1}^2 + k_{A_1+A_2 \rightarrow 2A_1} c_{A_1} c_{A_2} + \\ &\quad + k_{2A_2 \rightarrow A_1+A_2} \bar{c}_{A_2}^2 - k_{A_1+A_2 \rightarrow 2A_2} c_{A_1} c_{A_2} - \\ \dot{c}_{A_2} &= -k_{2A_1 \rightarrow A_1+A_2} \bar{c}_{A_1}^2 - k_{A_1+A_2 \rightarrow 2A_1} c_{A_1} c_{A_2} - \\ &\quad - k_{2A_2 \rightarrow A_1+A_2} \bar{c}_{A_2}^2 + k_{A_1+A_2 \rightarrow 2A_2} c_{A_1} c_{A_2} \end{aligned} \quad (2)$$

We now introduce the standard terminology of Chemical Reaction Network Theory (see [12], [5] for more details). We denote by $\mathbb{R}$ the set of real numbers, by $\mathbb{R}_+$ the set of strictly positive real numbers, and by $\mathbb{R}_{\geq}$ the set of nonnegative real numbers. For an arbitrary finite set I we denote by $\mathbb{R}^I$, $\mathbb{R}_+^I$ and $\mathbb{R}_{\geq}^I$ the sets of formal sums $\alpha = \sum_{i \in I} \alpha_i i$ with $\alpha_i \in \mathbb{R}$, $\alpha_i \in \mathbb{R}_+$ and $\alpha_i \in \mathbb{R}_{\geq}$, respectively. The support of an element $\alpha \in \mathbb{R}^I$ is $\text{supp}(\alpha) = \{i \in I : \alpha_i \neq 0\}$.

A *chemical reaction network* is a triple $(S, C, \mathcal{R})$, where S is the set of chemical species, $C \subseteq \mathbb{R}_{\geq}^S$ is the set of complexes (i.e., the objects on the left or right side of reaction arrows), and $\mathcal{R}$ is a relation on C , denoted $y \rightarrow y'$ and represents the set of reactions in the network. Moreover, the set $\mathcal{R}$ must satisfy the following three conditions: (i) it cannot contain elements of the form $y \rightarrow y$; (ii) for any $y \in C$ there exists some $y' \in C$ such that either $y \rightarrow y'$ or $y' \rightarrow y$; (iii) the union of the supports of all $y \in C$ is S .

For the network (1), the set of species is $S = \{A_1, A_2\}$, the set of complexes is $C = \{2A_1, A_1 + A_2, 2A_2\}$ and the set of reactions is $\mathcal{R} = \{2A_1 \rightleftharpoons A_1 + A_2, 2A_2 \rightleftharpoons A_1 + A_2\}$, and consists of 5 reactions, represented as two reversible reactions and one irreversible reaction.

Note that we regard the complexes as non-negative linear combinations of the species; on the other hand, it will be useful to also think of the complexes as (column) vectors of dimension equal to the number of elements of S , via an identification given by a fixed ordering of the species. For example, the complexes above are

$$2A_1 = \begin{bmatrix} 2 \\ 0 \end{bmatrix}, A_1 + A_2 = \begin{bmatrix} 1 \\ 1 \end{bmatrix}, \text{ and } 2A_2 = \begin{bmatrix} 0 \\ 2 \end{bmatrix}.$$

This slight abuse of notation provides a convenient way of representing the reaction vectors $y' - y$ for all $y \rightarrow y' \in \mathcal{R}$.

We may now define mass-action systems and the set of differential equations that governs mass-action kinetics. First we introduce a useful notation. Given two vectors $u = \sum_{i \in S} u_i i$ and $v = \sum_{i \in S} v_i i$ in $\mathbb{R}_{\geq}^S$, we denote $u^v = \prod_{i \in S} (u_i)^{v_i}$, with the convention $0^0 = 1$.

A *mass-action system* is a quadruple $(S, C, \mathcal{R}, k)$, where $(S, C, \mathcal{R})$ is a chemical reaction network and $k \in \mathbb{R}_{\geq}^S$, where $k_{y \rightarrow y'}$ is the *reaction rate constant* of the reaction $y \rightarrow y' \in \mathcal{R}$. The system of differential equations for the mass-action

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