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Fixed points in conjunctive networks and maximal independent sets in graph contractions

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ABSTRACT

Given a graph G, viewed as a loop-less symmetric digraph, we study the maximum number of fixed points in a conjunctive boolean network with G as interaction graph. We prove that if G has no induced C_4, then this quantity equals both the number of maximal independent sets in G and the maximum number of maximal independent sets among all the graphs obtained from G by contracting some edges. We also prove that, in the general case, it is coNP-hard to decide if one of these equalities holds, even if G has a unique induced C_4.

1. Introduction

A *Boolean network* with n components is a discrete dynamical system usually defined as a map

$$f : \{0,1\}^n \to \{0,1\}^n, \qquad x = (x_1, \dots, x_n) \mapsto f(x) = (f_1(x), \dots, f_n(x)).$$

Boolean networks have many applications. In particular, they are classical models for the dynamics of gene networks [21,35–37,20], neural networks [23,17,12,14,13] and social interactions [27,15]. They are also essential tools in information theory, for the binary network coding problem [32,10,9].

In many contexts, the main parameter of f is its *interaction graph*, the digraph G on $\{1, \dots, n\}$ that contains an arc from j to i if f_i depends on x_j. The arcs of G can also be signed by a labeling function σ, to obtain the *signed interaction graph* G_σ. The sign $\sigma(j,i)$ of an arc from j to i then indicates whether the Boolean function f_i is an increasing (positive sign), decreasing (negative sign) or non-monotone (zero sign) function of x_j. More formally, denoting e_j the jth base vector,

$$\sigma(j,i) = \begin{cases} 1 & \text{if } f_i(x) \le f_i(x+e_j) \text{ for all } x \in \{0,1\}^n \text{ with } x_j = 0, \\ -1 & \text{if } f_i(x) \ge f_i(x+e_j) \text{ for all } x \in \{0,1\}^n \text{ with } x_j = 0, \\ 0 & \text{otherwise.} \end{cases}$$

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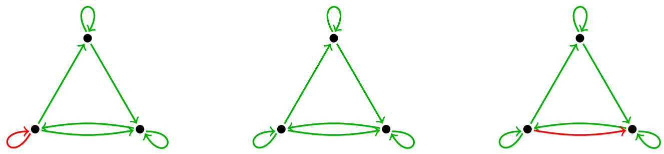

Fig. 1. Green arcs are positive, and red arcs are negative. This convention is used throughout the paper. (For interpretation of the references to color in this figure, the reader is referred to the web version of this article.)

The signed interaction graph is very commonly considered when studying gene networks, since a gene can typically either activate (positive sign) or inhibit (negative sign) another gene. Furthermore, the signed interaction graph is usually the first reliable information that biologists obtain when they study a gene network, the actual dynamics being much more difficult to determine [37,22]. A central problem is then to predict these dynamics according to the signed interaction graph. Among the many dynamical properties that can be studied, fixed points are of special interest since they correspond to stable states and have often specific meaning. For instance, in the context of gene networks, they correspond to stable patterns of gene expression at the basis of particular cellular processes [36,2]. Many works have thus been devoted to the study of fixed points. In particular, the number of fixed points has been the subject of a stream work, e.g. in [33,4,29,3,18,10,38,5,8]. Below, we denote by $\phi(G_\sigma)$ the *maximum number of fixed points* in a Boolean network with G_σ as signed interaction graph.

Positive and negative cycles The sign of a cycle in G_σ is *positive* (resp. *negative*) if the product of the signs of its arcs is non-negative (resp. non-positive). Positive cycles are key structures for the study of $\phi(G_\sigma)$. A fundamental result concerning this quantity, proposed by the biologist René Thomas, is that $\phi(G_\sigma) \leq 2$ if G_σ has only negative cycles. This was generalized in [3] into the following upper-bound, referred as the *positive feedback bound* in the following: for any signed digraph G_σ,

$$\phi(G_\sigma) \leq 2^{\tau^+(G_\sigma)},$$

where $\tau^+(G_\sigma)$ is the minimum size of a *positive feedback vertex set*, that is, the minimum size of a subset of vertices intersecting every positive cycle of G_σ. An immediate consequence is that $\max_\sigma \phi(G_\sigma) \leq 2^{\tau(G)}$ for all digraphs G, where $\tau(G)$ is the minimum size of a feedback vertex set of G. It is worst noting that this result has been proved independently in the context of network coding in information theory [32]. Actually, a central problem in this context, called the *binary network coding problem*, is equivalent to identify the digraphs G reaching the bound, that is, such that $\max_\sigma \phi(G_\sigma) = 2^{\tau(G)}$ [32,10].

The positive feedback bound is very perfectible. For instance, it is rather easy to find, for any k, a strongly connected signed digraph G_σ with $\phi(G_\sigma) = 1$ and $\tau^+(G_\sigma) \geq k$ [31]. This is not so surprising, since the positive feedback bound depends only on the structure of positive cycles, while negative cycles may have a strong influence on fixed points. Actually, such a gap, with $\phi(G_\sigma)$ bounded and $\tau(G_\sigma)$ unbounded, *requires* the presence of negative cycles, since one can prove the following: there exists an unbounded function $h : \mathbb{N} \to \mathbb{N}$ such that, for any strongly connected signed digraph G_σ with only positive cycles, $\phi(G_\sigma) \geq h(\tau^+(G_\sigma))$.[4]

In this situation, it is natural to focus our attention on the influence of negative cycles. A natural framework for this problem is to fix G and study the variation of $\phi(G_\sigma)$ according to labeling function σ, which gives the repartition of signs on the arcs of G. This is, however, a difficult problem, widely open, with very few formal results (see however [5,8]). This comes from the versatility of negative cycles: depending on the way they are connected to positive cycles, that can either be favorable or unfavorable to the presence of many fixed points. The simple example in Fig. 1 illustrates this. As another illustration, consider K_n^+ (resp. K_n^-), the signed digraphs obtained from K_n, the complete loop-less symmetric digraph on n vertices, by adding a positive (resp. negative) sign to each arc. It has been proved in [8] that, for any $n \geq 4$,

$$\phi(K_n^-) = \binom{n}{\lfloor \frac{n}{2} \rfloor} > \frac{2^{n+1}}{n+2} \geq \phi(K_n^+). \tag{1}$$

In K_n^-, the sign of every cycle is given by the parity of its length, and there is thus a balance between the number of positive and negative cycles. This balance allows the presence of more fixed points than in K_n^+, where all the cycles are positive. Actually, we may think that the balance obtained in K_n^- is optimal when zero sign is forbidden, that is, any Boolean network whose signed interaction graph is obtained from K_n by adding a positive or negative sign on each arc has at most $\phi(K_n^-)$ fixed points.

[4] First, if G_σ is strongly connected and has only positive cycles, then $\tau^+(G_\sigma) = \tau(G)$, and, by [24, Proposition 1], $\text{fix}(G_\sigma) = \text{fix}(G_+)$, where G_+ is obtained from G_σ by making positive all the arcs. Second, according to [6, Lemma 6], we have $\nu(G) < \phi(G_+)$, where $\nu(G)$ is the maximal size of a collection of vertex-disjoint cycles in G. Third, by a celebrated theorem of Reed, Robertson, Seymour and Thomas [28], there exists an unbounded function $h : \mathbb{N} \to \mathbb{N}$ such that $\nu(G) \geq h(\tau(G))$. We then deduce that $\phi(G_\sigma) = \phi(G_+) > \nu(G) \geq h(\tau(G)) = h(\tau^+(G_\sigma))$.