Network Inference

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Boolean Network Inference

Given a set of desirable properties (specifications, observations, ...);
The goal is to find all models that satisfy the properties.

There is no "universal strategy" for dynamical model inference, in the fashion of model checking for formal verification.
We therefore focus directly on the Boolean network scenario.

Specification:

(Over-approximated) interaction graph. In gene regulation, interactions and their sign can often be obtained from prior biological knowledge, e.g. transcriptomics databases.

Observations:

Time series measurements. The dynamical constraints typically come in the form of partially specified reachability relation. The observation is often incomplete (only values for a subset of variables are available).

Network Ensemble

Instead of trying each possible model separately, all plausible models are examined together, in an ensemble, to avoid repeated exploration of shared behaviours.

A Boolean network ensemble consists of all Boolean networks that share an interaction graph, and multiple techniques have been developed to analyse such ensembles:

- Coloured Model Checking;

  J. Barnat, L. Brim, A. Krejčí, A. Streck, D. Šafránek, M. Vejnár, and T. Vejpustek. On parameter synthesis by parallel model checking.
  IEEE/ACM Trans. Comput. Biol. Bioinformatics, 9(3):693–705, May 2012

- Symbolic Representation;

  G. Bernot, J.-P. Comet, and O. Roux. A genetically modified hoare logic that identifies the parameters of a gene network.
  In O. Roux and J. Bourdon, editors, *Computational Methods in Systems Biology*, pages 8–12, Cham, Switzerland, 2015. Springer International Publishing

- Answer Set Programming;

  S. Chevalier, C. Froidevaux, L. Paulevé, and A. Zinovyev. Synthesis of boolean networks from biological dynamical constraints using answer-set programming.
  In *2019 IEEE 31st International Conference on Tools with Artificial Intelligence (ICTAI)*, pages 34–41, 2019

Our Approach

J. Kolčák, D. Šafránek, S. Haar, and L. Paulevé. Parameter space abstraction and unfolding semantics of discrete regulatory networks.

Theoretical Computer Science, 765:120–144, 2019

Combination of symbolic representation of the admissible models and symbolic representation of the transition system.

The admissible models are abstracted by an application of **abstract interpretation**, representing a lattice by upper and lower bounds.

The transition system is abstracted by the construction of an unfolding, or rather a complete finite prefix of one.

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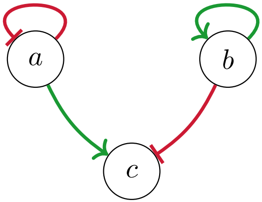
The transition system is abstracted by the construction of an unfolding, or rather a complete finite prefix of one.

We need a partial order on the set of admissible Boolean networks (a lattice of Boolean networks).

Parametrisation



$f_a(\mathbf{x}) = ?$
$f_b(\mathbf{x}) = ?$
$f_c(\mathbf{x}) = ?$

$\mathbf{x}_a$	$f_a(\mathbf{x})$	
0	$p^a_{\langle a=0 \rangle}$	
1	$p^a_{\langle a=1 \rangle}$	

$\mathbf{x}_b$	$f_b(\mathbf{x})$	
0	$p^b_{\langle b=0 \rangle}$	
1	$p^b_{\langle b=1 \rangle}$	

$\mathbf{x}_a$	$\mathbf{x}_b$	$f_c(\mathbf{x})$	
0	0	$p^c_{\langle a=0,b=0 \rangle}$	
1	0	$p^c_{\langle a=1,b=0 \rangle}$	
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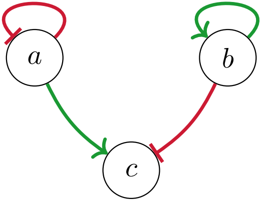
Parametrisation



$f_a(\mathbf{x}) = ?$
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$f_c(\mathbf{x}) = ?$

$\mathbf{x}_a$	$f_a(\mathbf{x})$	
0	$p^a_{\langle a=0 \rangle}$	$= p^{a}_{\emptyset}$
1	$p^a_{\langle a=1 \rangle}$	$= p^{a}_{\{a\}}$

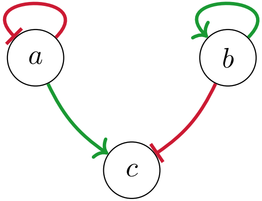
$\mathbf{x}_b$	$f_b(\mathbf{x})$	
0	$p^b_{\langle b=0 \rangle}$	
1	$p^b_{\langle b=1 \rangle}$	

$\mathbf{x}_a$	$\mathbf{x}_b$	$f_c(\mathbf{x})$	
0	0	$p^c_{\langle a=0, b=0 \rangle}$	
1	0	$p^c_{\langle a=1, b=0 \rangle}$	$= p^c_{\{a\}}$
0	1	$p^c_{\langle a=0, b=1 \rangle}$	$= p^c_{\{b\}}$
1	1	$p^c_{\langle a=1, b=1 \rangle}$	$= p^c_{\{a, b\}}$

Each **parameter** represents the output of one of the local functions for a possible input configuration.

A **parametrisation** is a vector $\mathbf{p} \in \mathbb{B}^{\sum_{i \in \{1,\dots,n\}} (2^{|\omega(i)|})} = \mathbb{B}^m$ assigning a value to each parameter.

Parametrisation



$\mathbf{x}_a$	$f_a(\mathbf{x})$	$\mathbf{p}$ $= p'$
0	$p^a_{\langle a=0 \rangle}$	1
1	$p^a_{\langle a=1 \rangle}$	0

$\mathbf{x}_b$	$f_b(\mathbf{x})$	$\mathbf{p}$ $= p'$
0	$p^b_{\langle b=0 \rangle}$	0
1	$p^b_{\langle b=1 \rangle}$	1

$\mathbf{x}_a$	$\mathbf{x}_b$	$f_c(\mathbf{x})$	$\mathbf{p}$	p'
0	0	$p^c_{\langle a=0,b=0 \rangle}$	0	1
1	0	$p^c_{\langle a=1,b=0 \rangle}$	1	1
0	1	$p^c_{\langle a=0,b=1 \rangle}$	0	0
1	1	$p^c_{\langle a=1,b=1 \rangle}$	0	1

$$f_a(\mathbf{x}) = \neg \mathbf{x}_a$$
$$f_b(\mathbf{x}) = \mathbf{x}_b$$
$$f_c(\mathbf{x}) = \mathbf{x}_a \wedge \neg \mathbf{x}_b \qquad x_a \vee \neg x_b$$

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A **parametrisation** is a vector $\mathbf{p} \in \mathbb{B}^{\sum_{i \in \{1,\dots,n\}} (2^{|\omega(i)|})} = \mathbb{B}^m$ assigning a value to each parameter.

$\mathbf{p} = (1, 0, 0, 1, 0, 1, 0, 0)$ $\qquad p' = (1, 0, 0, 1, 1, 1, 0, 1)$

Extreme Parameters

We extend the notation on variables interacting with any variable $i \in \{1, \ldots, n\}$ based on interaction signs:

Let $\omega^+(i) \triangleq \{j \in \omega(i) \mid j \xrightarrow{+} i \in E\}$ be the set of all variables that have a positive interaction with i (**activators** of i).

And $\omega^-(i) \triangleq \{j \in \omega(i) \mid j \xrightarrow{-} i \in E\}$ be the set of all variables that have a negative interaction with i (**inhibitors** of i).

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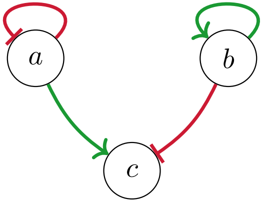
Assume a variable $i \in \{1, \ldots, n\}$ such that f_i is locally monotonic in all inputs, $\omega^+(i) \cap \omega^-(i) = \emptyset$.

Then the parameter $p^i_{\omega^+(i)}$ is the **maximum parameter**, and has to be equal to 1, $p^i_{\omega^+(i)} = 1$.

And the parameter $p^i_{\omega^-(i)}$ is the **minimum parameter**, and has to be equal to 0, $p^i_{\omega^-(i)} = 0$.

Extreme Parameters – Example



$\mathbf{x}_a$	$f_a(\mathbf{x})$	
0	$p^a_{\langle a=0\rangle}$	
1	$p^a_{\langle a=1\rangle}$	

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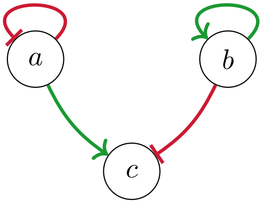

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$$\omega^+(a) = \emptyset$$

$$\omega^+(b) = \{b\}$$

$$\omega^+(c) = \{a\}$$

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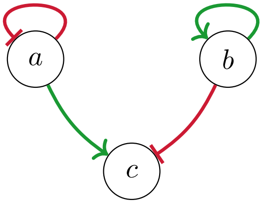

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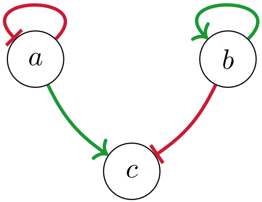

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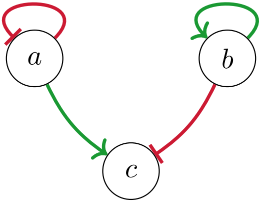
Extreme Parameters – Example



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$$\omega^+(b) = \{b\} \qquad \omega^-(b) = \emptyset$$

$$\omega^+(c) = \{a\} \qquad \omega^-(c) = \{b\}$$

Order on Parametrisations

Piecewise order on Boolean vectors of length m, $\mathbb{B}^m$.

Given two parametrisations $\mathbf{p}, \mathbf{p}' \in \mathbb{B}^m$,
$\mathbf{p} \leq \mathbf{p}' \overset{\Delta}{\Longleftrightarrow} \forall j \in \{1, \ldots, m\}, \mathbf{p}_j \leq \mathbf{p}'_j$.

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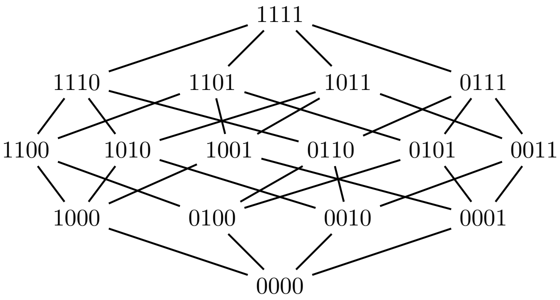

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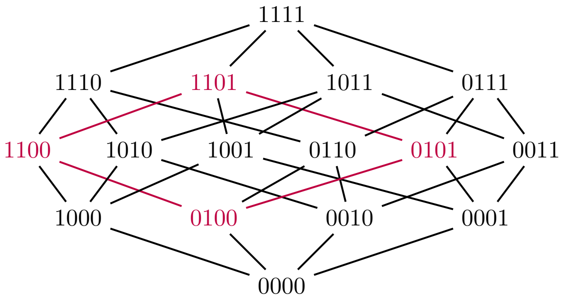
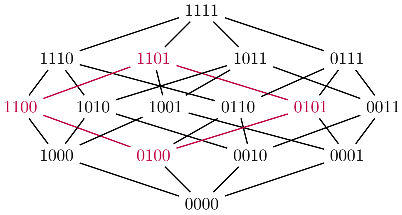


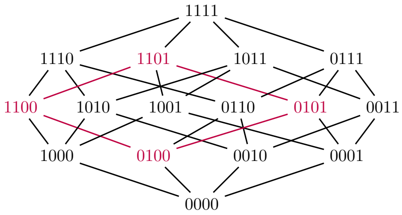
Lower and Upper Bounds



$\langle \mathbf{l} = 0100, \mathbf{u} = 1101 \rangle$

The lower and upper bound abstraction has two very useful properties.

Lower and Upper Bounds



$$\langle \mathbf{l} = 0100, \mathbf{u} = 1101 \rangle$$

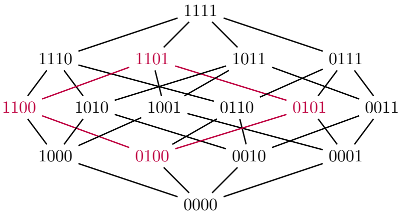
The lower and upper bound abstraction has two very useful properties.

1. Possible transitions can be enumerated without having the expand the abstraction.

$$\mathbf{x} \xrightarrow{async} \mathbf{x}^{\bar{i}} \Leftrightarrow$$
$$\exists \mathbf{p} \in \mathcal{P}, \mathbf{p}_{i,\mathbf{x}|_{\omega(i)}} = 1 - \mathbf{x}_i$$

$$\mathbf{x} \xrightarrow{async} \mathbf{x}^{\bar{i}} \Leftrightarrow$$
$$\mathbf{l}_{i,\mathbf{x}|_{\omega(i)}} = 1 - \mathbf{x}_i \vee \mathbf{u}_{i,\mathbf{x}|_{\omega(i)}} = 1 - \mathbf{x}_i$$

Lower and Upper Bounds



$$\langle \mathbf{l} = 0100, \mathbf{u} = 1101 \rangle$$

The lower and upper bound abstraction has two very useful properties.

1. Possible transitions can be enumerated without having the expand the abstraction.
2. The abstraction is of constant size.

$$\mathbf{x} \xrightarrow{async} \mathbf{x}^{\bar{i}} \Leftrightarrow$$
$$\exists \mathbf{p} \in \mathcal{P}, \mathbf{p}_{i,\mathbf{x}|_{\omega(i)}} = 1 - \mathbf{x}_i$$

$$\mathcal{O}(2^m)$$

$$\mathbf{x} \xrightarrow{async} \mathbf{x}^{\bar{i}} \Leftrightarrow$$
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$$\mathcal{O}(2m)$$

Galois Connection

Abstract Interpretation

The set $2^{\mathbb{B}^m}$ of all subsets of parametrisations is ordered by the set inclusion relation. Concrete set

We define a partial order on the set $\mathbb{B}^m \times \mathbb{B}^m$ of all pairs of parametrisations to be $\langle \mathbf{l}, \mathbf{u} \rangle \leq \langle \mathbf{l}', \mathbf{u}' \rangle \overset{\Delta}{\iff} \mathbf{l} \geq \mathbf{l}' \wedge \mathbf{u} \leq \mathbf{u}'$. Abstract set

We can define the abstraction by the means of a pair of functions, $\alpha \colon 2^{\mathbb{B}^m} \to \mathbb{B}^m \times \mathbb{B}^m$, called the **abstraction** function, and $\gamma \colon \mathbb{B}^m \times \mathbb{B}^m \to 2^{\mathbb{B}^m}$, the **concretisation** function.

$$\alpha \colon \mathcal{P} \mapsto \left\langle \bigwedge \mathcal{P}, \bigvee \mathcal{P} \right\rangle \qquad \gamma \colon \langle \mathbf{l}, \mathbf{u} \rangle \mapsto \{ \mathbf{p} \in \mathbb{B}^m \mid \mathbf{l} \leq \mathbf{p} \leq \mathbf{u} \}$$

The pair α, γ is called a **Galois connection** iff for all $\mathcal{P} \in 2^{\mathbb{B}^m}$ and all $\langle \mathbf{l}, \mathbf{u} \rangle \in \mathbb{B}^m \times \mathbb{B}^m$ it satisfies:

$$\alpha(\mathcal{P}) \leq \langle \mathbf{l}, \mathbf{u} \rangle \iff \mathcal{P} \subseteq \gamma(\langle \mathbf{l}, \mathbf{u} \rangle)$$

$P \leq \gamma(\alpha(P))$

Galois Connection

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$$\alpha(\mathcal{P}) \leq \langle \mathbf{l}, \mathbf{u} \rangle \iff \mathcal{P} \subseteq \gamma(\langle \mathbf{l}, \mathbf{u} \rangle)$$

An abstraction (over-approximation) defined by the means of a Galois connection is always **sound** – “produces no false negatives”.

Transition System of a Network Ensemble

The state set is the set of all configurations enriched with abstracted parametrisation sets: $\mathbb{S} = \mathbb{B}^n \times \mathbb{B}^m \times \mathbb{B}^m$.

The transitions are then given by the law defined earlier:

$$(\mathbf{x}, \langle \mathbf{l}, \mathbf{u} \rangle) \xrightarrow{async} (\mathbf{x}^{\bar{\mathbf{i}}}, \Lambda_o(\Lambda_m(\langle \mathbf{l}', \mathbf{u}' \rangle))) \iff \mathbf{l}_i = 1 - \mathbf{x}_i \vee \mathbf{u}_i = 1 - \mathbf{x}_i$$

where $\mathbf{l}' = \begin{cases} \mathbf{l}^{\overline{i,\mathbf{x}|_{\omega(i)}}} & \text{if } \mathbf{x}_i = 0 \wedge \mathbf{l}_{i,\mathbf{x}|_{\omega(i)}} = 0 \\ \mathbf{l} & \text{if } \mathbf{x}_i = 1 \vee \mathbf{l}_{i,\mathbf{x}|_{\omega(i)}} = 1 \end{cases}$,

$\mathbf{u}' = \begin{cases} \mathbf{u} & \text{if } \mathbf{x}_i = 0 \vee \mathbf{u}_{i,\mathbf{x}|_{\omega(i)}} = 0 \\ \mathbf{u}^{\overline{i,\mathbf{x}|_{\omega(i)}}} & \text{if } \mathbf{x}_i = 1 \wedge \mathbf{u}_{i,\mathbf{x}|_{\omega(i)}} = 1 \end{cases}$

and the narrowing operators $\Lambda_m, \Lambda_o \colon \mathbb{B}^m \times \mathbb{B}^m \to \mathbb{B}^m \times \mathbb{B}^m$, ensuring tightness of the abstraction with respect to monotonicity and existence (observability) of the interactions, are defined on the following slides.

Monotonicity Narrowing

We define a partial order on the parameters of variable $i \in \{1, \dots, n\}$ as $p^i_q \leq p^i_{q'} \overset{\Delta}{\iff} q \cap \omega^+(i) \subseteq q' \cap \omega^+(i) \wedge q \cap \omega^-(i) \supseteq q' \cap \omega^-(i)$.

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The narrowing operator $\Lambda_m \colon \mathbb{B}^m \times \mathbb{B}^m \to \mathbb{B}^m \times \mathbb{B}^m$ is then defined as:

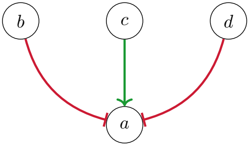
$$\Lambda_m \colon \langle \mathbf{l}, \mathbf{u} \rangle \mapsto \langle \mathbf{l}', \mathbf{u}' \rangle$$

where for each $i \in \{1, \dots, n\}$ and each $q \in 2^{\omega(i)}$:

$$\mathbf{l}'_{i,q} = \mathtt{max}_{q' \leq q}(\mathbf{l}_{i,q'})$$

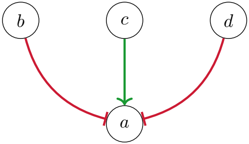
$$\mathbf{u}'_{i,q} = \mathtt{min}_{q' \geq q}(\mathbf{u}_{i,q'})$$

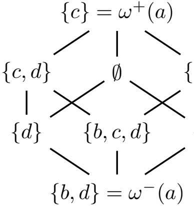
Monotonicity Narrowing – Example



b	c	d	**l**	**u**	**l**′	**u**′
0	0	0	0	0		
1	0	0	0	1		
0	1	0	0	1		
1	1	0	1	1		
0	0	1	0	1		
1	0	1	0	1		
0	1	1	0	1		
1	1	1	0	1		

Monotonicity Narrowing – Example





b	c	d	**l**	**u**	**l**$'$	**u**$'$
0	0	0	0	0		
1	0	0	0	1		
0	1	0	0	1		
1	1	0	1	1		
0	0	1	0	1		
1	0	1	0	1		
0	1	1	0	1		
1	1	1	0	1		

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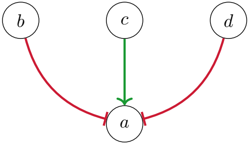
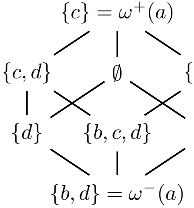


b	c	d	**l**	**u**	**l′**	**u′**
0	0	0	0	0	0	
1	0	0	0	1	0	
0	1	0	0	1	1	
1	1	0	1	1	1	
0	0	1	0	1	0	
1	0	1	0	1	0	
0	1	1	0	1	0	
1	1	1	0	1	0	



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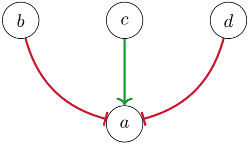

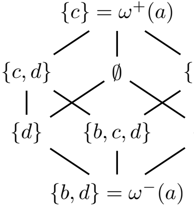

b	c	d	$\mathbf{l}$	$\mathbf{u}$	$\mathbf{l}'$	$\mathbf{u}'$
0	0	0	0	0	0	0
1	0	0	0	1	0	0
0	1	0	0	1	1	1
1	1	0	1	1	1	1
0	0	1	0	1	0	0
1	0	1	0	1	0	0
0	1	1	0	1	0	1
1	1	1	0	1	0	1

Closed and Open Parameters

A parameter p_q^i is closed in $\langle \mathbf{l}, \mathbf{u} \rangle$ iff $\mathbf{l}_{i,q} = \mathbf{u}_{i,q}$.
Conversely, p_q^i is open iff $\mathbf{l}_{i,q} < \mathbf{u}_{i,q}$.

The subset $q \subseteq \omega(i) \setminus \{j\}$ is a closed context for $j \in \omega(i)$ iff both p_q^i and $p_{q\cup\{j\}}^i$ are closed. A context which is not closed is open. We use $C_i^j(\langle \mathbf{l}, \mathbf{u} \rangle) = \{q \in 2^{\omega(i)\setminus\{j\}} \mid \mathbf{l}_{i,q} = \mathbf{u}_{i,q} \wedge \mathbf{l}_{i,q\cup\{j\}} = \mathbf{u}_{i,q\cup\{j\}}\}$ and $O_i^j(\langle \mathbf{l}, \mathbf{u} \rangle) = \{q \in 2^{\omega(i)\setminus\{j\}} \mid \mathbf{l}_{i,q} < \mathbf{u}_{i,q} \vee \mathbf{l}_{i,q\cup\{j\}} < \mathbf{u}_{i,q\cup\{j\}}\}$ to denote the sets of all closed and open contexts of j, respectively, in $\langle \mathbf{l}, \mathbf{u} \rangle$.

Finally, a closed context q is observable if $\mathbf{l}_{i,q} \neq \mathbf{l}_{i,q\cup\{j\}}$, that is, if the context is closed with a different value depending on the inclusion of j. Let $oC_i^j(\langle \mathbf{l}, \mathbf{u} \rangle) = \{q \in C_i^j(\langle \mathbf{l}, \mathbf{u} \rangle) \mid \mathbf{l}_{i,q} \neq \mathbf{l}_{i,q\cup\{j\}}\}$ be the set of all observable closed contexts of j in $\langle \mathbf{l}, \mathbf{u} \rangle$.

Observability Narrowing

The narrowing operator $\Lambda_o \colon \mathbb{B}^m \times \mathbb{B}^m \to \mathbb{B}^m \times \mathbb{B}^m$ is defined as $\Lambda_o \colon \langle \mathbf{l}, \mathbf{r} \rangle \mapsto \langle \mathbf{l}', \mathbf{u}' \rangle$ where

$$\mathbf{l}' = \begin{cases} \mathbf{l}^{\overline{i,q}} & \text{if } oC_i^j(\langle \mathbf{l}, \mathbf{u} \rangle) = \emptyset \wedge O_i^j(\langle \mathbf{l}, \mathbf{u} \rangle) = \{q\} \wedge \mathbf{u}_{i,q \cup \{j\}} = 0 \\ \mathbf{l}^{\overline{i,q \cup \{j\}}} & \text{if } oC_i^j(\langle \mathbf{l}, \mathbf{u} \rangle) = \emptyset \wedge O_i^j(\langle \mathbf{l}, \mathbf{u} \rangle) = \{q\} \wedge \mathbf{u}_{i,q} = 0 \\ \mathbf{l} & \text{otherwise} \end{cases}$$

$$\mathbf{u}' = \begin{cases} \mathbf{u}^{\overline{i,q}} & \text{if } oC_i^j(\langle \mathbf{l}, \mathbf{u} \rangle) = \emptyset \wedge O_i^j(\langle \mathbf{l}, \mathbf{u} \rangle) = \{q\} \wedge \mathbf{l}_{i,q \cup \{j\}} = 1 \\ \mathbf{u}^{\overline{i,q \cup \{j\}}} & \text{if } oC_i^j(\langle \mathbf{l}, \mathbf{u} \rangle) = \emptyset \wedge O_i^j(\langle \mathbf{l}, \mathbf{u} \rangle) = \{q\} \wedge \mathbf{l}_{i,q} = 1 \\ \mathbf{u} & \text{otherwise} \end{cases}$$