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Electronic version of an article published as International Journal of Bifurcation and Chaos, 31, 11, 2021, 10.1142/S0218127421300329 © World Scientific Publishing Company <https://doi.org/10.1142/S0218127421300329>

# STABILITY AND BIFURCATIONS OF EQUILIBRIA IN NETWORKS WITH PIECEWISE LINEAR INTERACTIONS

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In this paper we study equilibria of differential equation models for networks. When interactions between nodes are taken to be piecewise constant, an efficient combinatorial analysis can be used to characterize the equilibria. When the piecewise constant functions are replaced with piecewise linear functions, the equilibria are preserved as long as the piecewise linear functions are sufficiently steep. Therefore the combinatorial analysis can be leveraged to understand a broader class of interactions. To better understand how broad this class is, we explicitly characterize how steep the piecewise linear functions must be for the correspondence between equilibria to hold. To do so, we analyze the steady state and Hopf bifurcations which cause a change in the number or stability of equilibria as slopes are decreased. Additionally, we show how to choose a subset of parameters so that the correspondence between equilibria holds for the smallest possible slopes when the remaining parameters are fixed.

*Keywords:* Regulatory Network, Bifurcation, Switching System, Cyclic Feedback System

## 1. Introduction

An analysis of dynamics of systems of differential equations (ODE) forms a bedrock of modeling of complex systems ranging from natural sciences to social sciences and, most recently, in data science. General questions are notoriously difficult, as three dimensional ODE systems can exhibit chaotic dynamics. Fortunately, in many applications in biology the structure of interactions between chemical species or organisms is captured by a directed graph, called a *regulatory network*, and each pairwise interaction can be modeled by a monotone bounded function. However, there is usually not much additional information about the precise shape of these nonlinearities; they do not come from first principle physical models. Matching quantitative predictions of such models to experimental data and/or predicting outcomes of an experiment therefore requires precise experimental measurements of all interaction nonlinearities or sufficient preliminary data to fit parameters. Another approach is to predict qualitative features of the dynamics from the structural constraints given by the network and which are valid for an entire class of uncertain nonlinearities. The aim of this paper is to further develop mathematical methods used in the latter approach.

This paper uses a methodology based on a particular class of interaction nonlinearities called *switching functions*. These functions are piece-wise constant with a single threshold  $\theta$  and take either a lower value  $L$  or an upper value  $U$ . These switching systems of differential equations have been used as models of gene

regulatory networks since the 70’s [Glass & Kauffman, 1973; Glass & Pasternack, 1978; de Jong, 2002; Thomas, 1991; Edwards, 2001; Cummins *et al.*, 2016; Ironi *et al.*, 2011; Gedeon, 2020]. However, using these functions as the right hand side of an ODE system presents several technical challenges, especially how to deal with the fact that the vector field is not defined at thresholds  $\theta$ . The idea of the newer DSGRN (Dynamic Signatures Generated by Regulatory Networks) approach [Cummins *et al.*, 2016; Gedeon *et al.*, 2018; Gedeon, 2020], supported by a suite of corresponding software [Cummins *et al.*, 2020], is to capture information about the network dynamics given by switching system models in the form of combinatorial (finite) data, and then use this data to rigorously establish results about well-defined dynamics of ODE’s with continuous right hand side that are a small perturbation of the switching functions. We have shown in a previous paper [Duncan *et al.*, 2021] that when switching functions are replaced with smooth *sigmoidal functions* which are within a  $C^0$  neighborhood of the switching functions, all equilibria and their stability of the resulting system can be inferred from the combinatorial data.

This work is devoted to addressing the quantitative question of how big this neighborhood is, i.e. how far sigmoidal functions can be perturbed from switching functions and still maintain the same equilibria and their stability. We formulate this problem as bifurcation problem: how far can we perturb switching functions before there must be a bifurcation resulting in loss of stability or a loss of an equilibrium? The immediate challenge is that this question, as stated, is too broad since there is no good parameterization of all sigmoidal functions. We therefore restrict our attention to a particular subclass of sigmoidal functions that are easy to parameterize and where bifurcations are easier to track - *ramp* functions. Ramp functions have two constant parts which have values (in agreement with the corresponding switching function)  $L$  and  $U$ , and the sharp transition at the threshold of the switching function is replaced by a linear ramp that joins these two parts over an interval of length  $2\varepsilon$ . This  $\varepsilon$ , or alternatively the slope of the ramp  $\frac{|U-L|}{2\varepsilon}$ , are natural parameters that measure how far a ramp function is from a switching function.

Our results provide, for a given network structure, explicit bounds on  $\varepsilon$  across all ramp nonlinearities that guarantee the persistence of all switching system equilibria and their stability. Using theory of bifurcations of piecewise linear systems we explicitly describe the steady-state bifurcations (i.e saddle node and pitchfork) and Hopf bifurcations that lead to disappearance of the equilibria or a change in their stability as the steepness of the linear portion of the ramp functions decrease. We also solve an optimization problem where we fix values of  $L$  and  $U$  for all switching nonlinearities but optimize the placement of thresholds  $\theta$  that maximizes the critical  $\varepsilon$  across all such placements.

There are two areas of applications of this work. One is in the area of gene regulatory networks. As an example, we mention epithelial-mesenchymal transition (EMT) [Jolly *et al.*, 2016; Hong *et al.*, 2015] which is responsible for phenotype switching between epithelial phenotype where cells are a part of well organized tissue, and mesenchymal phenotype in which cells can travel to other tissues through the bloodstream. EMT is thought to be responsible for emergence of cancer metastasis. In an earlier work [Xin *et al.*, 2020] we used DSGRN to scan over the entire 42 dimensional space of parameters of the EMT network and found parameters where the switching system ODE has up to 8 stable equilibria. While two of these equilibria correspond to pure epithelial and mesenchymal states, the others correspond to so called *intermediate* states. The number and characterization of these states is a hotly debated issue in cancer systems biology, since they may correspond to phenotypes that are more aggressive and have poorer clinical outcomes. Results of this paper can be used to establish how many of these intermediate states occur in ODE models with ramp function nonlinearities with moderate steepness. This is motivated by the fact that biologically realistic exponents in Hill function models are usually assumed to be in the range of 2 – 4.

Our result may be of interest in deep learning community. Echo state networks [Jaeger & Haas, 2004] have roots in recurrent artificial neural networks (rANN), that were introduced by Hopfield [Hopfield, 1982] and Grossberg [Grossberg, 1988] almost 40 years ago. While there are many implementations of echo state networks under many different names, the main structure is a network whose nodes are connected by weighted directed edges, where each node processes the collection of input through a nonlinear function (binary, sigmoidal, or a ramp). For these networks, our work provides a characterization of the number and stability of equilibria for steep ramp functions, with explicit bounds on their steepness, based on the structure of the network.

## 2. The Regulatory Network and Switching Systems

[Cummins *et al.*, 2016]. A *regulatory network*  $\mathbf{RN} = (V, E)$  is an annotated finite directed graph with vertices  $V = \{1, \dots, N\}$  called *network nodes* and directed edges  $E \subset V \times V \times \{1, -1\}$ . An annotated edge  $(j, i, +1)$  represents an *activation* of node  $i$  by node  $j$  and is denoted  $j \rightarrow i$ ; annotated edge  $(j, i, -1)$  represents *repression* of node  $i$  by node  $j$  and is denoted  $j \dashv i$ . We write  $\mathbf{s}_{ij} = 1$  if  $j \rightarrow i$  and  $\mathbf{s}_{ij} = -1$  if  $j \dashv i$ . We indicate either  $j \rightarrow i$  or  $j \dashv i$  without specifying which by writing  $(j, i) \in E$ . We allow self edges, but admit at most one edge between any two nodes. The set of *sources* and *targets* of a node are denoted by

$$\mathbf{S}(k) = \{j \mid (j, k) \in E\} \quad \text{and} \quad \mathbf{T}(k) = \{j \mid (k, j) \in E\}.$$

To an  $\mathbf{RN}$  we associate a *switching system* of the form

$$\dot{x} = -\Gamma x + \Lambda(x) \quad (1)$$

where  $\Gamma$  is a diagonal matrix with entries  $\Gamma_{jj} = \gamma_j$  and  $\Lambda$  is a nonlinear function of the form

$$\Lambda_i(x) := \prod_{\ell=1}^{p_i} \sum_{j \in I_\ell} \sigma_{ij}(x_j) \quad (2)$$

with  $I_1, \dots, I_{p_i}$  a partition of  $\mathbf{S}(i)$ . Each  $\sigma_{ij}$  is a *switching function* of the form

$$\sigma_{ij}(x_j) := \begin{cases} L_{ij}, & \mathbf{s}_{ij} = 1 \text{ and } x_j < \theta_{ij} \text{ or } \mathbf{s}_{ij} = -1 \text{ and } x_j > \theta_{ij} \\ U_{ij}, & \mathbf{s}_{ij} = 1 \text{ and } x_j > \theta_{ij} \text{ or } \mathbf{s}_{ij} = -1 \text{ and } x_j < \theta_{ij} \\ \text{undefined,} & \text{if } x_j = \theta_{ij}. \end{cases} \quad (3)$$

The parameter  $Z = (L, U, \theta, \Gamma)$ , where  $L := (L_{ij})$ ,  $U := (U_{ij})$ ,  $\theta := (\theta_{ij})$  are vectors indexed by  $(ij)$ , is the *switching parameter*. We denote a switching system parameterized by  $Z$  by  $\text{SWITCH}(Z)$ .

To the same network  $\mathbf{RN}$  we also associate a *ramp system*,  $\mathcal{R}(Z, \varepsilon)$ , where  $Z$  is a switching parameter and  $\varepsilon \in \mathbf{R}^{N \times N}$  is a *perturbation parameter*. We say  $\varepsilon' \leq \varepsilon$  or  $\varepsilon' < \varepsilon$  when the component-wise comparisons  $\varepsilon'_{ij} \leq \varepsilon_{ij}$  or  $\varepsilon'_{ij} < \varepsilon_{ij}$  hold for each  $(j, i) \in E$ , respectively. The dynamics of a ramp system are defined by

$$\dot{x} = -\Gamma x + \mathbf{R}(x; \varepsilon) \quad (4)$$

where  $\mathbf{R}$  is defined by

$$\mathbf{R}_i(x; \varepsilon) := \prod_{\ell=1}^{p_i} \sum_{j \in I_\ell} R_{ij}(x_j; \varepsilon_{ij}) \quad (5)$$

and  $R_{ij}$  is a *ramp function* of the form

$$R_{ij}(x_j; \varepsilon_{ij}) := \begin{cases} L_{ij}, & \mathbf{s}_{ij} = 1 \text{ and } x_j < \theta_{ij} - \varepsilon_{ij} \text{ or } \mathbf{s}_{ij} = -1 \text{ and } x_j > \theta_{ij} + \varepsilon_{ij} \\ U_{ij}, & \mathbf{s}_{ij} = 1 \text{ and } x_j > \theta_{ij} + \varepsilon_{ij} \text{ or } \mathbf{s}_{ij} = -1 \text{ and } x_j < \theta_{ij} - \varepsilon_{ij} \\ \frac{U_{ij} + L_{ij}}{2} + s_{ij} m_{ij} (x_j - \theta_{ij}), & \theta_{ij} - \varepsilon_{ij} \leq x_j \leq \theta_{ij} + \varepsilon_{ij} \end{cases} \quad (6)$$

and  $m_{ij} := \frac{U_{ij} - L_{ij}}{2\varepsilon_{ij}}$ . We call the pair  $(Z, \varepsilon)$  a *ramp parameter*.

*Example.* Throughout the paper we will illustrate the concepts on a simple example of a two node network we call the *positive toggle switch*, where the two nodes mutually activate each other, i.e.

$$\mathbf{RN} = (V, E) = (\{1, 2\}, \{(1 \rightarrow 2), (2 \rightarrow 1)\}).$$

We chose the name positive toggle switch for its resemblance to the toggle switch introduced in [Gardner *et al.*, 2000], in which the nodes mutually repress each other rather than activate. The associated switching system has the form

$$\begin{aligned} \dot{x}_1 &= -\gamma_1 x_1 + \sigma_{12}(x_2) \\ \dot{x}_2 &= -\gamma_2 x_2 + \sigma_{21}(x_1) \end{aligned}$$

where  $s_{12} = s_{21} = 1$ . The associated ramp system has the form

$$\begin{aligned}\dot{x}_1 &= -\gamma_1 x_1 + R_{12}(x_2; \varepsilon_{12}) \\ \dot{x}_2 &= -\gamma_2 x_2 + R_{21}(x_1; \varepsilon_{21}).\end{aligned}$$

### 3. Equilibria of Ramp Systems

Both switching systems and a ramp systems have an associated cell complex which we call the *switching complex* and *ramp complex*, respectively. As defined in [Duncan *et al.*, 2021], a cell complex is a partition of phase space  $\overline{\mathbf{R}}_+^N$  generated by a threshold set. Each cell in a cell complex is defined by choosing either an interval with end points defined by consecutive thresholds or a threshold singleton for each direction. The threshold sets and corresponding complexes for switching and ramp systems are defined below. See Figure 1 for the switching and ramp complexes for the positive toggle.

#### Definition 3.1.

- (1) For each  $j \in V$ , we define  $\theta_{-\infty j} := 0$ ,  $\theta_{\infty j} := \infty$ ,  $\varepsilon_{-\infty j} := 0$ ,  $\varepsilon_{\infty j} := 0$ , and

$$\Theta_j(Z, \varepsilon) := \{\theta_{ij} \pm \varepsilon_{ij} > 0 \mid i \in \mathbf{T}(j)\} \cup \{\theta_{\infty j}, \theta_{-\infty j}\}.$$

The *ramp threshold set* is the collection  $\Theta(Z, \varepsilon) := (\Theta_1(Z, \varepsilon), \dots, \Theta_N(Z, \varepsilon))$  and  $\Theta(Z, 0)$  is the threshold set for a switching system.

- (2) A cell  $\tau$  associated to the threshold set  $\Theta(Z, \varepsilon)$  is a product of  $k \leq N$  thresholds and  $N - k$  open intervals whose end points are consecutive thresholds. That is, after reordering the variables a cell can be written as

$$\tau = \prod_{j=1}^k \{\zeta_{i_j j}\} \times \prod_{j=k+1}^N (\zeta_{a_j j}, \zeta_{b_j j}).$$

where  $\zeta_{i_j j}, \zeta_{a_j j}, \zeta_{b_j j} \in \Theta_j(Z, \varepsilon)$  for each  $j$ . The cell is *regular* if  $k = 0$  and *singular* otherwise. We let  $\pi_j(\tau)$  denote the projection of  $\tau$  onto the  $j$ th direction and say  $j$  is a *singular direction* of  $\tau$  if  $\pi_j(\tau)$  is a singleton and a *regular direction* if  $\pi_j(\tau)$  is an interval. We denote the set of singular directions by  $\text{sd}(\tau)$ .

- (3) The *ramp complex*  $\chi(\Theta(Z, \varepsilon))$  is the collection of cells associated to the threshold set  $\Theta(Z, \varepsilon)$ . When  $\varepsilon = 0$ , we call the cell complex  $\chi(\Theta(Z, 0))$  the *switching complex*. When the switching parameter  $Z$  is clear from context we will write  $\chi(\varepsilon)$  for the ramp complex and  $\chi(0)$  for the switching complex.

Given a ramp system, we are interested in determining the location of equilibria by identifying the regular cell they belong to. That is, we are not concerned with determining the precise value of an equilibrium but rather in which cell  $\tau$  the equilibrium is contained. Note that since the ramp system is affine in each regular cell, each such cell can contain at most one equilibrium.

**Definition 3.2.** Let  $(Z, \varepsilon)$  be a ramp parameter. If  $\tau \in \chi(\varepsilon)$  contains an equilibrium of  $\mathcal{R}(Z, \varepsilon)$ , then  $\tau$  is a  *$\mathcal{R}$ -equilibrium cell*.

For switching systems, equilibrium cells are defined differently because making an arbitrarily small perturbation of a switching system into a system with a continuous right hand side may introduce new equilibria. Therefore we define SWITCH-equilibrium cells to be those cells for which the equilibria of a continuous system, where this system is taken from some class of continuous systems, limits to. These cells  $\tau \in \chi(0)$  can be singular. In this paper we take the class of continuous systems in the definition to be ramp systems, although in [Duncan *et al.*, 2021] a larger class of sigmoidal systems were used. Theorem 11, together with the characterization of SWITCH-equilibrium cells given by Theorem 3.11 of [Duncan *et al.*, 2021], imply that the collection of equilibrium cells defined by using these two classes of systems is the same.

**Definition 3.3.** [Duncan *et al.*, 2021] Let  $\tau \in \chi(0)$ . If there is an  $A \in \mathbf{R}_+^{N \times N}$  so that for all  $\varepsilon < A$ , a ramp system  $\mathcal{R}(Z, \varepsilon)$  has a fixed point  $x^\varepsilon$  satisfying  $x^\varepsilon \rightarrow \tau$  as  $\varepsilon \rightarrow 0$ , then  $\tau$  is a *SWITCH-equilibrium cell*. If  $\tau$  is a singular cell, then  $x^\varepsilon$  is a *singular stationary point* (SSP).

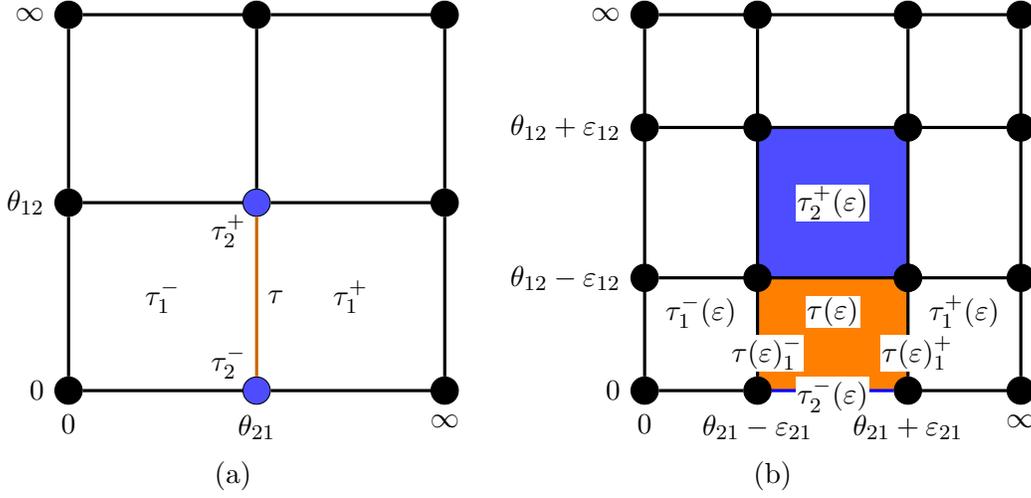


Fig. 1. **Complexes  $\chi(0)$ ,  $\chi(\varepsilon)$ , and neighbors in the positive toggle switch example.** (a): Complex  $\chi(0)$ . Each box, line, and point is a cell. The cell  $\tau = \{\theta_{21}\} \times (0, \theta_{12})$  is indicated by the orange line. For  $\tau$ , the direction 1 is singular and the direction 2 is regular. The 2-neighbors of  $\tau$ , (see Definition 5.5)  $\tau_2^+$  and  $\tau_2^-$ , are indicated by the blue circles while the 1-neighbors,  $\tau_1^-$  and  $\tau_1^+$ , are the labeled two dimensional cells. (b): Complex  $\chi(\varepsilon)$ . Cell  $\tau(\varepsilon)$  is indicated by the orange box and  $\tau_2^+(\varepsilon)$  by the blue box. The cell  $\tau_2^-(\varepsilon) = \tau(\varepsilon)_2^-$  is the labeled blue line. Cells  $\tau(\varepsilon)_1^+$  and  $\tau(\varepsilon)_1^-$  are the labeled vertical lines.

Theorem 3.11 of [Duncan *et al.*, 2021] shows that SWITCH-equilibrium cells can be identified solely from a list of inequalities between parameters. In Theorem 1, we give an explicit upper bound on the size of the perturbation parameter  $\varepsilon$  so that there is a one-to-one correspondence between  $\mathcal{R}$ -equilibrium cells and SWITCH-equilibrium cells. Together, these theorems can be used to identify all  $\mathcal{R}$ -equilibrium cells provided  $\varepsilon$  satisfies the bound.

### 3.1. Weak Equivalence of Ramp and Switching Parameters

This section describes a relationship between the ramp complex and switching complex that holds when  $\varepsilon$  is small enough. Small enough is made precise by the notion of *weak equivalence*, which we define after the following non-degeneracy condition which we will assume throughout the remainder of this paper.

**Definition 3.4.** [Duncan *et al.*, 2021]. The switching parameter  $Z$  is *threshold regular* if

- For all  $(j, i) \in E$ ,  $\theta_{ij} > 0$ , and
- for all  $j \in V$ ,  $i_1, i_2 \in \mathbf{T}(j)$ ,  $\theta_{i_1 j} \neq \theta_{i_2 j}$ .

**Definition 3.5.** Consider a threshold regular switching parameter  $Z$ . For  $j \in V$ , denote the ordering of the thresholds  $\{\theta_{ij} \pm \varepsilon_{ij} \mid i \in \mathbf{T}(j)\}$  by  $O_j(Z, \varepsilon)$ . The *order parameter* is the collection of these orders,  $O(Z, \varepsilon) = (O_1(Z, \varepsilon), \dots, O_N(Z, \varepsilon))$ . We say the ramp parameter  $(Z, \varepsilon)$  is *weakly equivalent* to the switching parameter  $Z$ , denoted  $Z \sim_W (Z, \varepsilon)$ , if  $O(Z, \varepsilon) = O(Z, \varepsilon')$  for all  $\varepsilon' < \varepsilon$ .

Weak equivalence implies the existence of a bijection between the regular cells of the ramp complex and the cells of the switching complex. Let

$$\chi_0 = \chi(0) \setminus \{\tau \in \chi(0) \mid \exists j \in V, \pi_j(\tau) \subset \{\theta_{-\infty j}, \theta_{\infty j}\}\}$$

be the cells that do not lie on the boundary of the positive orthant  $\mathbf{R}_+^N$ . When  $Z \sim_W (Z, \varepsilon)$ , there is a bijection that maps cells in  $\chi_0$  to  $N$ -dimensional cells in  $\chi(\varepsilon)^{(N)}$

$$\phi^\varepsilon : \chi_0 \rightarrow \chi(\varepsilon)^{(N)}, \quad \phi^\varepsilon = (\phi_1^\varepsilon, \dots, \phi_n^\varepsilon)$$

defined by

$$\phi_j^\varepsilon(\tau) \mapsto \begin{cases} (\theta_{i_j j} - \varepsilon_{i_j j}, \theta_{i_j j} + \varepsilon_{i_j j}), & j \in \text{sd}(\tau), \pi_j(\tau) = \{\theta_{i_j j}\} \\ (\theta_{a_j j} + \varepsilon_{a_j j}, \theta_{b_j j} - \varepsilon_{b_j j}), & j \notin \text{sd}(\tau), \pi_j(\tau) = (\theta_{a_j j}, \theta_{b_j j}). \end{cases}$$

See Figure 1(b) for illustration. Note that if  $O(Z, \varepsilon) = O(Z, \varepsilon')$ , then  $\phi^{\varepsilon, \varepsilon'} := (\phi^\varepsilon)^{-1} \circ \phi^{\varepsilon'}$  is a bijection between  $\chi(\varepsilon)^{(N)}$  and  $\chi(\varepsilon')^{(N)}$ .

While  $\phi^\varepsilon$  is a bijection, the map  $\phi^{\varepsilon, \varepsilon'}$  can be extended to a homeomorphism. The map  $\phi^\varepsilon$  preserves the following property: if  $\tau$  is a neighbor (defined precisely in Definition 5.5) of  $\kappa$  in  $\chi_0$  then  $N$  dimensional cells  $\phi^\varepsilon(\tau)$  and  $\phi^\varepsilon(\kappa)$  share an  $N - 1$  dimensional boundary in  $\chi(\varepsilon)$ .

We can extend  $\phi^\varepsilon$  to all cells,  $\tau \in \chi(0)$ , through the map  $\tilde{\phi}^\varepsilon : \chi(0) \rightarrow \chi(\varepsilon)$  defined by

$$\tilde{\phi}_j^\varepsilon(\tau) \mapsto \begin{cases} \pi_j(\tau), & \pi_j(\tau) \subset \{\theta_{-\infty j}, \theta_{\infty j}\} \\ \phi_j^\varepsilon(\tau), & \text{otherwise.} \end{cases} \quad (7)$$

Given  $\tau \in \chi(0)$ , we define  $\tau(\varepsilon) := \tilde{\phi}^\varepsilon(\tau)$ . For a cell  $\tau \in \chi(0)$  of a two node regulatory network, Figure 1(a) shows its neighbors. The corresponding cell  $\tau(\varepsilon)$  and its neighbors are depicted in 1(b).

### 3.2. The Combinatorial Parameter and Strong Equivalence

Having provided a relationship between the switching and ramp complexes, we now proceed to relate the dynamics of the two systems. This is accomplished by generalizing the notion of *combinatorial parameter*, introduced in [Cummins *et al.*, 2016] for switching systems, to ramp systems. In [Cummins *et al.*, 2016], combinatorial parameters are equivalence classes of switching parameters which generate the same global dynamics of (1) as described by a state transition graph for the system. Here we extend combinatorial parameters to include ramp parameters with non-zero  $\varepsilon$  such that the equilibrium cells are the same within each equivalence class. To do so, we first define the set of non-degenerate ramp parameters over which the equivalence classes will be defined.

#### Definition 3.6.

- (1) The ramp parameter  $(Z, \varepsilon)$  is *regular* if
  - $Z$  is threshold regular,
  - for all  $(j, i) \in E$ ,  $0 < L_{ij} < U_{ij}$ ,
  - for all  $k \in V$ ,  $\gamma_k > 0$ , and
  - for all  $\kappa \in \chi(0)^{(N)}$  and  $(j, i) \in E$ ,  $\gamma_j(\theta_{ij} \pm \varepsilon_{ij}) \neq \Lambda_j(\kappa)$  for each threshold  $\theta_{ij}$  which defines  $\kappa$ .
- (2) The switching parameter  $Z$  is *regular* if (1) holds with  $\varepsilon = 0$ .

This definition for regular switching parameters coincides with the definition for regular parameters in [Cummins *et al.*, 2016]. We now proceed to define combinatorial parameters.

#### Definition 3.7.

Consider a regular ramp parameter  $(Z, \varepsilon)$ .

- (1) The *input combinations* of the  $i$ th node is the Cartesian product

$$\text{In}_i := \prod_{j \in \mathbf{S}(i)} \{\text{off}, \text{on}\}.$$

The *indicator function*,  $\mathbb{1}_i : \mathbf{R}_+^{\mathbf{S}(i)} \rightarrow \text{In}_i$ , is defined component-wise by

$$\mathbb{1}_{ij}(x) := \begin{cases} \text{off}, & \mathbf{s}_{ij} = 1 \text{ and } x_j < \theta_{ij} \text{ or } \mathbf{s}_{ij} = -1 \text{ and } x_j > \theta_{ij} \\ \text{on}, & \mathbf{s}_{ij} = 1 \text{ and } x_j > \theta_{ij} \text{ or } \mathbf{s}_{ij} = -1 \text{ and } x_j < \theta_{ij} \\ \text{undefined}, & \text{otherwise.} \end{cases}$$

The  $\sigma$ -valuation function,  $v_i : \mathbf{In}_i \rightarrow \mathbf{R}^{\mathbf{S}^{(i)}}$ , is defined by

$$v_{ij}(A) := \begin{cases} L_{ij}, & A_j = \text{off} \\ U_{ij}, & A_j = \text{on} \\ \text{undefined}, & \text{otherwise.} \end{cases}$$

Note that  $\sigma_{ij} = v_{ij} \circ \mathbb{1}_{ij}$ . The  $\Lambda$ -valuation function,  $\omega_i : \mathbf{In}_i \rightarrow \mathbf{R}$ , is defined by

$$\omega_i(A) := \prod_{\ell=1}^{p_i} \sum_{j \in I_\ell} v_{ij}(A).$$

Note that  $\Lambda_i = \omega_i \circ \mathbb{1}_i$ .

Define  $\mathbf{L}_j : \mathbf{In}_j \times \mathbf{T}(j) \times \{-, +\} \times \mathbf{R}_+^{N \times N} \rightarrow \{-1, 1\}$  by

$$\mathbf{L}_j(A, i, \pm; \varepsilon) := \text{sgn}(-\gamma_j(\theta_{ij} \pm \varepsilon_{ij}) + \omega_j(A)).$$

When  $\varepsilon = 0$  we drop the ' $\pm$ ' argument. The *logic parameter* is the collection  $\mathbf{L}(Z, \varepsilon) := (\mathbf{L}_1(\cdot, \cdot, \cdot; \varepsilon), \dots, \mathbf{L}_N(\cdot, \cdot, \cdot; \varepsilon))$ .

- (2) We define an equivalence relation  $(Z, \varepsilon) \sim (Z', \varepsilon')$  whenever  $(\mathbf{L}(Z', \varepsilon'), O(Z', \varepsilon')) = (\mathbf{L}(Z, \varepsilon), O(Z, \varepsilon))$ . The *combinatorial parameter* is an equivalence class under  $\sim$  and is denoted by  $\mathcal{P}(Z, \varepsilon)$ . In other words,  $(Z', \varepsilon') \in \mathcal{P}(Z, \varepsilon)$  whenever  $(\mathbf{L}(Z', \varepsilon'), O(Z', \varepsilon')) = (\mathbf{L}(Z, \varepsilon), O(Z, \varepsilon))$ .

We use the combinatorial parameter to define a notion of *strong equivalence* between a ramp parameter and a switching parameter.

**Definition 3.8.** Let  $(Z, \varepsilon)$  be a regular ramp parameter. The switching parameter  $Z$  and  $(Z, \varepsilon)$  are *strongly equivalent*, denoted  $Z \sim_S (Z, \varepsilon)$ , if for all  $\varepsilon' < \varepsilon$ ,  $\mathcal{P}(Z, \varepsilon) = \mathcal{P}(Z, \varepsilon')$ .

Note that strong equivalence implies weak equivalence. The power of strong equivalence is that it not only allows identification of cells in  $\chi(0)$  with cells in  $\chi(\varepsilon)$ , but in addition allows us to use knowledge about the dynamics of  $\text{SWITCH}(Z)$  to make inferences about the dynamics of  $\mathcal{R}(Z, \varepsilon)$ . This is made precise in Section 7.

*Example.* Consider a two node regulatory network defined by

$$\mathbf{RN} = (V, E) = (\{1, 2\}, \{(1, 2), (2, 1), (2, 2)\})$$

at a switching parameter  $Z$  satisfying

$$L_{12} < \theta_{21} < U_{12} \quad \text{and} \quad L_{21}L_{22} < \theta_{12} < L_{21}U_{22} < \theta_{22} < U_{21}L_{22} < U_{21}U_{22}.$$

For strong equivalence  $Z \sim_S (Z, \varepsilon)$  to hold, all of the thresholds of the ramp system must obey the same inequalities, i.e.

$$L_{12} < \theta_{21} - \varepsilon_{21} < \theta_{21} + \varepsilon_{21} < U_{12}, \quad \text{and} \\ L_{21}L_{22} < \theta_{12} - \varepsilon_{12} < \theta_{12} + \varepsilon_{12} < L_{21}U_{22} < \theta_{22} - \varepsilon_{22} < \theta_{22} + \varepsilon_{22} < U_{21}L_{22} < U_{21}U_{22}.$$

For weak equivalence  $Z \sim_W (Z, \varepsilon)$  to hold, only the inequalities between thresholds need to be satisfied, i.e.

$$\theta_{12} + \varepsilon_{12} < \theta_{22} - \varepsilon_{22}.$$

Weak equivalence but not strong equivalence can be satisfied if, for example,

$$\theta_{21} - \varepsilon_{21} < L_{12} < \theta_{21} + \varepsilon_{21} < U_{12}, \quad \text{and} \\ L_{21}L_{22} < \theta_{12} - \varepsilon_{12} < \theta_{12} + \varepsilon_{12} < L_{21}U_{22} < \theta_{22} - \varepsilon_{22} < U_{21}L_{22} < \theta_{22} + \varepsilon_{22} < U_{21}U_{22}.$$

### 3.3. Characterization of $\mathcal{R}$ -Equilibrium Cells

First we note that the proof of Theorem 3.11 in [Duncan *et al.*, 2021] could be modified to show that there is a unique ramp equilibrium limiting to each SWITCH-equilibrium cell. However, the structure of ramp systems allows us to improve on the theorem by obtaining an explicit upper bound on  $\varepsilon$  so that the correspondence between SWITCH-equilibrium cells and ramp equilibria is maintained. The proof can be found in Section 7.

**Theorem 1.** *Let  $Z \sim_S (Z, \varepsilon)$ . Then  $\sigma \in \chi(\varepsilon)$  is an  $\mathcal{R}$ -equilibrium cell if and only if  $\sigma = \tau(\varepsilon)$  for some SWITCH-equilibrium cell  $\tau \in \chi(0)$ .*

*Moreover, if an equilibrium exists in a cell  $\tau(\varepsilon)$ , or in a cell  $\tau$ , then it is unique. If  $\tau \in \chi(0)$  is a regular equilibrium cell then the equilibrium of SWITCH( $Z$ ) in  $\tau$ , as well as the corresponding equilibrium of  $\mathcal{R}(Z, \varepsilon)$  in  $\tau(\varepsilon)$ , are stable.*

## 4. Stability and Bifurcations of Equilibria in Cyclic Feedback Networks

In this section we study a special class of systems called cyclic feedback systems (CFS). As shown in [Duncan *et al.*, 2021], any switching system can be locally decomposed into a product of cyclic feedback systems. A key theorem in Section 5 shows that a similar decomposition holds for weakly equivalent ramp systems. This allows us to generalize results for ramp CFS to general ramp systems. Therefore, we first study stability and bifurcations of equilibria in CFS in this section and then generalize the results to general networks in Section 5.

**Definition 4.1.** A *cyclic feedback network* (CFN) is a regulatory network  $\mathbf{RN} = (V, E)$  with  $N$  nodes such that  $E = \{(1, 2), (2, 3), \dots, (N-1, N), (N, 1)\}$ . A *cyclic feedback system* (CFS) is switching or ramp system associated to a CFN. The network  $\mathbf{RN}$  is a *positive* (resp. *negative*) CFN if  $\mathbf{RN}$  is a CFN and  $\prod_j s_{(j+1)j} = 1$  (resp.  $\prod_j s_{(j+1)j} = -1$ ).

Given a  $\mathbf{RN}$  is a CFN, we assume without loss of generality that each edge  $(j, j+1)$  of a CFN is activating, i.e.  $s_{(j+1)j} = 1$ , except possibly for the edge  $(N, 1)$ . This can be done because every CFN can be put into this form via a change of variables [Gedeon & Mischaikow, 1994]. Given a ramp CFS,  $\mathcal{R}(Z, \varepsilon)$ , we let  $M(\varepsilon) := \prod_j m_{(j+1)j}(\varepsilon_{(j+1)j})$  denote the product of the magnitude of the slopes of the ramp functions.

Vital to this discussion of equilibrium cells is the notion of a *loop characteristic cell*, defined below.

**Definition 4.2.** [Duncan *et al.*, 2021]. Given  $\tau \in \chi(0)$  we associate a map

$$\rho^\tau : V \rightarrow V, \quad \rho^\tau(j) = \begin{cases} i_j, & j \in \text{sd}(\tau) \\ j, & \text{otherwise} \end{cases}$$

and say  $\tau$  is a *loop characteristic cell* if  $\rho^\tau$  is a permutation on  $\text{sd}(\tau)$ . We denote the set of loop characteristic cells by LCC. Note that all  $N$ -dimensional cells  $\kappa \in \chi(0)$  are automatically loop characteristic cells, since  $\text{sd}(\kappa) = \emptyset$ . Therefore  $\chi^{(N)} \subset \text{LCC}$ .

We note that SWITCH-equilibrium cells are a subset of loop characteristic cells [Veflingstad & Plahte, 2007; Duncan *et al.*, 2021].

### 4.1. Stability of Equilibria for CFS

If strong equivalence holds for a ramp parameter, i.e.  $Z \sim_S (Z, \varepsilon)$ , then Theorem 1 implies that if  $\tau \in \chi(0)$  is a regular equilibrium cell, then the equilibrium in the cell  $\tau(\varepsilon)$  of the ramp system is stable. Here we address the case that  $\tau$  is a singular cell. If  $\tau(\varepsilon)$  contains an equilibrium and  $Z \sim_S (Z, \varepsilon)$  then  $\tau$  is a SWITCH-equilibrium cell and in particular  $\tau \in \text{LCC}$ . The only singular loop characteristic cell of a CFS is the cell defined by the intersection of all thresholds,  $\tau = \prod \{\theta_{(j+1)j}\}$ . If  $\tau$  is an equilibrium cell, then for  $\varepsilon$  small enough the equilibrium contained in  $\tau(\varepsilon)$  is stable if  $\mathbf{RN}$  is a negative CFN with  $N \leq 2$  and unstable otherwise [Ironi *et al.*, 2011; Duncan *et al.*, 2021]. In the case of a positive CFN, strong equivalence characterizes how large  $\varepsilon$  can be so that instability is maintained.

**Proposition 1.** *Let  $\mathbf{RN}$  be a positive CFN and  $Z$  be a switching parameter such that  $\tau \in \chi(0)$  is a singular equilibrium cell of  $\text{SWITCH}(Z)$ . If  $Z \sim_S (Z, \varepsilon)$  then the equilibrium of  $\mathcal{R}(Z, \varepsilon)$  in  $\tau(\varepsilon)$  is unstable.*

*Proof.* Let  $x \in \tau(\varepsilon)$ . According to Lemma 4.6 of [Duncan *et al.*, 2021], the characteristic polynomial of the Jacobian  $J(x; \varepsilon)$  satisfies

$$p(\lambda; x, \varepsilon) := (-1)^N (\det(J(x; \varepsilon) - \lambda I)) = \prod_{i=1}^N (\gamma_i + \lambda) - M(x, \varepsilon).$$

The coefficients of  $\lambda^k$  in the polynomial  $p(\lambda; x, \varepsilon)$  are all positive for  $k > 0$ . The coefficient of  $\lambda^0$  is negative when

$$\prod_{j=1}^N \gamma_j < M(\varepsilon).$$

Therefore, by Descartes' Rule of Signs,  $p(\lambda; x, \varepsilon)$  has a positive real root when the above inequality holds. By Proposition 4.8 of [Duncan *et al.*, 2021], there is an  $\varepsilon_0 \leq \varepsilon$  small enough so that  $p(\lambda; x, \varepsilon)$  has a positive real root.

Let  $\tilde{\varepsilon} : [0, 1] \rightarrow \mathbf{R}_+^{N \times N}$  be a continuous function such that  $\tilde{\varepsilon}(0) = \varepsilon_0$ ,  $\tilde{\varepsilon}(1) = \varepsilon$ , and  $\varepsilon_0 \leq \tilde{\varepsilon}(s) \leq \varepsilon$  for all  $s$ . By Theorem 1, for each  $s$ ,  $\mathcal{R}(Z, \tilde{\varepsilon}(s))$  contains a unique equilibrium in  $\tau(\tilde{\varepsilon}(s))$ . Since  $\mathcal{R}(Z, \tilde{\varepsilon}(s))$  is a linear system, the assumption  $\det(J(\tilde{\varepsilon}(s))) = 0$  would imply that there are infinitely many equilibria in  $\kappa(\tilde{\varepsilon}(s))$ . Therefore we conclude that for all  $s \in [0, 1]$ ,  $\det(J(\tilde{\varepsilon}(s))) \neq 0$ . Since the coefficient of  $\lambda^0$  in  $p(\lambda; x, \tilde{\varepsilon}(s))$  is  $(-1)^N \det(J(\tilde{\varepsilon}(s)))$ , the constant term of  $p$  never vanishes as  $s$  is varied and in particular it doesn't change sign. Therefore, the constant term of  $p(\lambda; x, \tilde{\varepsilon}(1))$  is negative so that  $p$  has a positive real root. So, if  $x \in \tau(\varepsilon)$  is an equilibrium,  $J(x; \varepsilon)$  has a positive eigenvalue and the equilibrium is unstable. ■

In the case that  $\mathbf{RN}$  is a negative cyclic feedback system with  $N > 2$ , it is possible that the unstable equilibrium undergoes a Hopf bifurcation for some choice of  $\varepsilon$  with  $Z \sim_S (Z, \varepsilon)$ . Therefore for negative CFN, although strong equivalence guarantees the existence of an equilibrium, as  $\varepsilon$  is increased the stability of the equilibrium may change before strong equivalence fails.

## 4.2. Border Crossing Bifurcations in CFS

We now address how the stability or existence of an equilibrium of a ramp CFS can change when it crosses a cell boundary. Our first two results address bifurcations that can occur at the point strong equivalence fails in a positive CFS. Proposition 2 shows that a saddle node bifurcation occurs when a regular equilibrium meets the singular equilibrium at a corner of  $\tau(\varepsilon)$  while Proposition 3 shows that a pitchfork bifurcation occurs when the regular equilibria meet opposite corners of  $\tau(\varepsilon)$ . After these results, we address the non-degenerate case of an equilibrium crossing a codimension one boundary of a cell. The proofs can be found in Section 8.

**Proposition 2.** *Let  $Z$  be a switching parameter and  $\mathbf{RN}$  be a positive cyclic feedback network such that  $\tau \in \chi(0)$  is a singular equilibrium cell. Suppose  $\varepsilon^0$  satisfies one of the following conditions*

- (1)  $\gamma_j(\theta_{(j+1)j} - \varepsilon_{(j+1)j}^0) = L_{j(j-1)}$  and  $\gamma_j(\theta_{(j+1)j} + \varepsilon_{(j+1)j}^0 s_{(j+1)j}) < U_{j(j-1)}$  or
- (2)  $\gamma_j(\theta_{(j+1)j} + \varepsilon_{(j+1)j}^0) = U_{j(j-1)}$  and  $\gamma_j(\theta_{(j+1)j} - \varepsilon_{(j+1)j}^0) > L_{j(j-1)}$

for each  $j$ . Then  $\mathcal{R}(Z, \varepsilon)$  has two stable equilibria and an unstable equilibrium for  $\varepsilon < \varepsilon^0$  and one stable equilibrium for  $\varepsilon > \varepsilon^0$  when  $\varepsilon - \varepsilon^0$  is sufficiently small. That is,  $\mathcal{R}(Z, \varepsilon)$  has a saddle node-like bifurcation at  $\varepsilon = \varepsilon^0$ .

While the previous proposition is a local result since we prove there is a single equilibrium when  $\varepsilon > \varepsilon^0$  if  $\varepsilon$  is close enough to  $\varepsilon^0$ , the next is a global one as it applies to all values of  $\varepsilon$  as long as all components of  $\varepsilon$  and  $\varepsilon_0$  satisfy the required inequality.

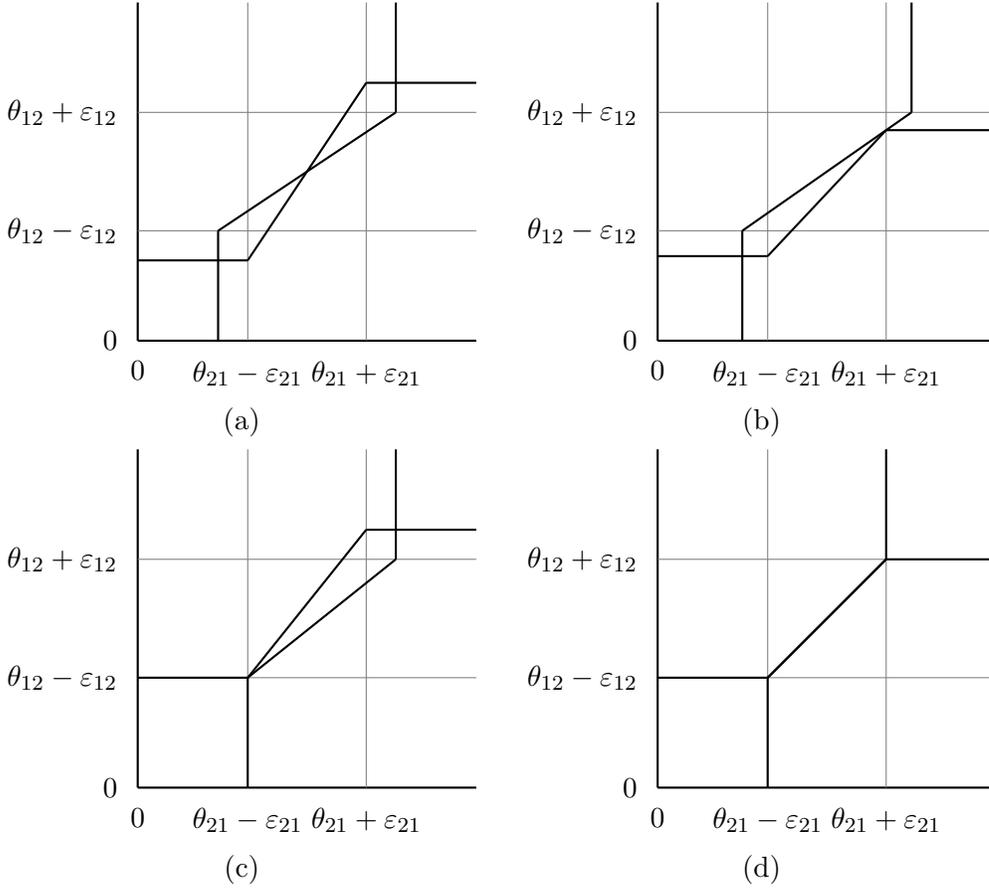


Fig. 2. **Nullclines for the positive toggle switch at a parameter  $Z$  with a central singular equilibrium cell  $\tau$ .** The switching parameter  $Z$  is chosen so that there are three SWITCH-equilibrium cells. **(a):**  $Z \sim_S (Z, \varepsilon)$  so there are three  $\mathcal{R}$ -equilibrium cells by Theorem 1. **(b):** The top right corner of the nullcline  $\gamma_2 x_2 = R_{21}(x_1; \varepsilon)$  is at the right boundary of  $\tau(\varepsilon)$ , resulting in a non-smooth saddle node by Theorem 2. **(c):** The bottom left corners of both nullclines are at the bottom left corner of  $\tau(\varepsilon)$ , resulting in a saddle-like bifurcation by Proposition 2. **(d):** Both corners of both nullclines are at a corner of  $\tau(\varepsilon)$ , resulting in the pitchfork-like bifurcation of Proposition 3.

**Proposition 3.** *Let  $\mathbf{RN}$  be a positive cyclic feedback network. Suppose  $\varepsilon^0$  satisfies*

$$\gamma_j(\theta_{(j+1)j} - \varepsilon_{(j+1)j}^0) = L_{j(j-1)} \quad \text{and} \quad \gamma_j(\theta_{(j+1)j} + \varepsilon_{(j+1)j}^0) = U_{j(j-1)}$$

*for each  $j$ . Then if  $\varepsilon < \varepsilon^0$ ,  $\mathcal{R}(Z, \varepsilon)$  has two stable equilibria and one unstable equilibrium and if  $\varepsilon > \varepsilon^0$ ,  $\mathcal{R}(Z, \varepsilon)$  has exactly one stable equilibrium. That is,  $\mathcal{R}(Z, \varepsilon')$  has a pitchfork-like bifurcation at  $\varepsilon = \varepsilon^0$ .*

To address the non-degenerate case, we use the theory of discontinuity induced bifurcations in piecewise smooth systems found in [Di Bernardo *et al.*, 2008]. Let  $(Z(s), \varepsilon(s))$  be a smooth parameterization of ramp parameters with  $\varepsilon(s) > 0$  for all  $s$ . Based on results in [Di Bernardo *et al.*, 2008], there are two possibilities:

- (1) The border crossing bifurcation is *persistent*: the equilibrium exists for both  $s < s_0$  and  $s > s_0$  although the stability may change at  $s_0$ .
- (2) The border crossing bifurcation is a *non-smooth saddle-node*. This bifurcation is analogous to a smooth saddle node bifurcation and occurs when an unstable equilibrium and a stable equilibrium collide and annihilate each other at the boundary.

**Theorem 2.** *Let  $\mathbf{RN}$  be a CFN. Consider a parameterization of ramp parameters  $(Z, \varepsilon)$  by a parameter  $s$ ,  $(Z(s), \varepsilon(s))$ . Suppose  $\mathcal{R}(Z(s), \varepsilon(s))$  has a non-degenerate border crossing bifurcation at  $x$  when  $s = s_0$ . Let  $\tau \in \chi(0)$  be the singular loop characteristic cell of  $\text{SWITCH}(Z(0))$ .*

- (1) If  $x \notin \partial\tau(\varepsilon(s^0))$  then the bifurcation is persistent and stability does not change.
- (2) If  $x \in \partial\tau(\varepsilon(s^0))$ , and  $\mathbf{RN}$  is a positive CFN, then the bifurcation is a non-smooth saddle node if  $M(\varepsilon(s_0)) > \prod \gamma_i$  and a stability preserving persistent bifurcation if  $M(\varepsilon(s_0)) < \prod \gamma_i$ .
- (3) If  $x \in \partial\tau(\varepsilon(s^0))$ ,  $\Gamma(s_0) = I$ , and  $\mathbf{RN}$  is a negative CFN, then the bifurcation is a stability changing persistent bifurcation if  $N > 2$  and  $M(\varepsilon(s_0)) > \sec(\pi/N)^N$  and a stability preserving persistent bifurcation if  $N \leq 2$  or  $M(\varepsilon(s_0)) < \sec(\pi/N)^N$ .

Figure 2 shows all possible bifurcations in a positive CFS which are given by Propositions 2 and 3, and Theorem 2. For the figure, we have chosen parameter  $Z$  in such a way that  $\tau$  is an equilibrium cell. For such  $Z$  the saddle node bifurcation in Figure 2(b) results in the annihilation of the unstable equilibrium in  $\tau$  and a stable equilibrium as the slopes are decreased. If parameter  $Z$  is chosen so that  $\tau$  is not an equilibrium, but only a singular loop characteristic cell, there can be saddle node bifurcations which create a stable and unstable equilibrium as the slopes are decreased.

On  $\tau(\varepsilon)$ , all ramp functions  $R_{(j+1)j}$  are operating in their linear regimes and we may write the dynamics as

$$\dot{x} = J(\varepsilon)x + b, \quad x \in \tau(\varepsilon) \quad (8)$$

where  $J(\varepsilon)$  is the Jacobian matrix of  $\mathcal{R}(Z, \varepsilon)$  evaluated at any  $x \in \tau(\varepsilon)$  and  $b$  is a vector depending on  $L$ ,  $U$ , and  $\theta$ . Generically,  $J(\varepsilon)$  is full rank so that  $J(\varepsilon)x = -b$  has a solution,  $x(\varepsilon)$ . If  $x(\varepsilon) \in \tau(\varepsilon)$ , then  $x(\varepsilon)$  is an equilibrium of  $\mathcal{R}(Z, \varepsilon)$ . If  $x(\varepsilon) \notin \tau(\varepsilon)$ , then, following [Di Bernardo *et al.*, 2008], we call  $x(\varepsilon)$  a *virtual equilibrium*. A consequence of Theorem 2 is that to detect steady state bifurcations in  $\mathcal{R}(Z(s), \varepsilon(s))$ , one only has to track this possibly virtual equilibrium  $x(\varepsilon(s))$  and the value of  $M(\varepsilon(s))$ . Knowledge of the equilibria in other cells is not necessary. In particular, we are often interested in ramp parameter parameterizations of the form  $(Z, \varepsilon(s))$  where  $\varepsilon(0) = 0$  and  $\varepsilon(s)$  is monotone increasing. In this context we ask for the minimum value of  $s$ , say  $s_0$ , so that the number or stability of equilibria of  $\mathcal{R}(Z, \varepsilon(s))$  changes. Theorem 2 implies that  $s_0$  is given by the minimum value of  $s$  so that  $x(\varepsilon(s)) \in \partial\tau(\varepsilon(s))$  or  $M(\varepsilon(s)) = \prod \gamma_i$  if the CFN is positive or  $M(\varepsilon(s)) = \sec(\pi/N)^N$  if the CFN is negative and  $\Gamma = 1$ . The perturbation parameter at  $s_0$ ,  $\varepsilon(s_0)$ , is then the largest value of  $\varepsilon$ , under the parameterization, such that the equilibria of  $\mathcal{R}(Z, \varepsilon)$  agree with those of SWITCH( $Z$ ).

## 5. Stability and Bifurcations in General Networks

In this section we extend the results of Section 4, which apply to cyclic feedback systems, to any regulatory network. This is done by first showing that near any loop characteristic cell  $\tau$ , there is a decomposition of  $\mathcal{R}(Z, \varepsilon)$  into a product of CFS and a diagonal system. Given this decomposition, the extensions immediately follow.

### 5.1. Local Decomposition into Cyclic Feedback Systems

The following definition allows us to precisely define the region of phase space on which the decomposition corresponding to a particular loop characteristic cell is valid.

**Definition 5.1.** For  $\tau \in \chi(0)$ , the *cell neighborhood* of  $\tau$ , denoted  $\mathcal{N}(\tau)$  is defined by

$$\mathcal{N}(\tau) := \{\kappa \in \chi(0) \mid \tau \subset \bar{\kappa}\}$$

where  $\bar{\kappa}$  is the closure of  $\kappa$ . We define the closure of the cells in  $\chi(\varepsilon)$  corresponding to  $\mathcal{N}(\tau)$  by

$$\mathcal{N}(\tau; \varepsilon) := \overline{\{\kappa(\varepsilon) \mid \kappa \in \mathcal{N}(\tau)\}}.$$

Although  $\mathcal{N}(\tau; \varepsilon)$  is a set of cells, we will often write  $x \in \mathcal{N}(\tau; \varepsilon)$  to indicate  $x \in \kappa$  for some  $\kappa \in \mathcal{N}(\tau; \varepsilon)$ .

Statements 1,2,4, and 5 of the following lemma were proven in [Duncan *et al.*, 2021], while statements 3 and 6 are implied by Lemma 6.

**Lemma 1.** *Let  $\tau \in \chi(0)$  and  $(j, i) \in E$  with  $i \neq \rho^\tau(j)$ . Assume  $Z \sim_W (Z, \varepsilon)$ . Then*

- (1)  $\sigma_{ij}(\tau)$  is well defined,
- (2) for all  $\kappa \in \mathcal{N}(\tau)$ , we have  $\sigma_{ij}(\kappa) = \sigma_{ij}(\tau)$  is independent of  $\kappa$ ,
- (3) for all  $x \in \mathcal{N}(\tau; \varepsilon)$ ,  $R_{ij}(x; \varepsilon) = \sigma_{ij}(\tau)$ .

Consequently if  $i \notin \{\rho^\tau(j) \mid j \in \text{sd}(\tau)\}$ , then

- (4)  $\Lambda_i(\tau)$  is well defined,
- (5) for all  $\kappa \in \mathcal{N}(\tau)$  we have  $\Lambda_i(\kappa) = \Lambda_i(\tau)$  is independent of  $\kappa$ ,
- (6) for all  $x \in \mathcal{N}(\tau; \varepsilon)$ ,  $R_i(x; \varepsilon) = \Lambda_i(\tau)$ .

In [Duncan *et al.*, 2021], it was shown that given a loop characteristic cell  $\tau \in \text{LCC}$ , on the cell neighborhood  $\mathcal{N}(\tau)$ , a switching system decomposes into a product of cyclic feedback systems and a diagonal system. The same holds for ramp systems  $\mathcal{R}(Z, \varepsilon)$  for which weak equivalence holds, i.e.  $Z \sim_W (Z, \varepsilon)$ . The CFNs associated to this decomposition can be determined from the cycles generating  $\rho^\tau$ . Let  $\rho^\tau|_{\text{sd}(\tau)} = (c_1, \dots, c_n)$  be the cycle decomposition of  $\rho^\tau$  restricted to the singular directions. Let  $\ell_d := \text{length}(c_d)$  and  $s_d := \sum_{j < d} \ell_j$ . We reorder the variables so that  $c_d$  acts on  $\{s_d + 1, s_d + 2, \dots, s_d + \ell_d\}$  and  $c_d(s_d + i) = s_d + i + 1$  for  $i < \ell_d$  and  $c_d(s_d + \ell_d) = s_d + 1$ . To each cycle  $c_d$  we associate the CFN

$$\mathbf{RN}^d := (V^d := \{s_d + 1, \dots, s_d + \ell_d\}, E^d := \{(j, c_d(j)) \mid j \in V^d\})$$

which is positive or negative according to

$$\text{sgn}(c_d) := \prod_{j=s_d+1}^{s_d+\ell_d} \mathbf{s}_{c_d(j)j}.$$

To construct the CFS associated to each CFN, let  $\ell_{n+1} := N - s_{n+1}$  be the number of regular directions and for each  $d = 1, \dots, n + 1$  define projections of the cell neighborhood  $\mathcal{N}(\tau; \varepsilon)$  and cells  $\kappa \in \mathcal{N}(\tau; \varepsilon)$  by

$$\mathcal{N}^d(\tau; \varepsilon) := \prod_{j=s_d+1}^{s_d+\ell_d} \pi_j(\mathcal{N}(\tau; \varepsilon)) \quad \text{and} \quad \kappa^d := \prod_{j=s_d+1}^{s_d+\ell_d} \pi_j(\kappa).$$

We set  $\mathbf{R}(\cdot; \varepsilon, \tau) := \mathbf{R}(\cdot; \varepsilon)|_{\mathcal{N}(\tau; \varepsilon)}$  to be the restriction of  $\mathbf{R}$  onto  $\mathcal{N}(\tau; \varepsilon)$ . We then define

$$\mathbf{R}^d(\cdot; \varepsilon, \tau) := (\mathbf{R}_{s_d+1}(\cdot; \varepsilon, \tau), \dots, \mathbf{R}_{s_d+\ell_d}(\cdot; \varepsilon, \tau))$$

to be the projection of the resulting function onto the directions of the  $d$ -th subsystem. Let  $\Gamma^d$  be the  $\ell_d \times \ell_d$  diagonal matrix with entries  $\Gamma_{ii} = \gamma_{s_d+i}$  for  $i = 1, \dots, \ell_d$ . The dynamics for the  $d$ th system, which we denote  $\mathcal{R}^d(Z, \varepsilon; \tau)$  is then given explicitly by

$$\dot{x}^d = -\Gamma^d x^d + \Lambda^d(x^d; \varepsilon, \tau), \quad x^d \in \mathcal{N}^d(\tau; \varepsilon)$$

where  $x^d = (x_{s_d+1}, \dots, x_{s_d+\ell_d})$ . Note that for  $d \leq n$ ,  $\mathcal{R}^d(Z, \varepsilon; \tau)$  is a CFS, while  $\mathcal{R}^{n+1}(Z, \varepsilon; \tau)$  is a diagonal system describing the dynamics of the regular variables. The following theorem is now a consequence of Lemma 1. For a full argument in the case  $\varepsilon = 0$ , see [Duncan *et al.*, 2021].

**Theorem 3.** *Let  $(Z, \varepsilon)$  be a ramp parameter with  $Z \sim_W (Z, \varepsilon)$  and  $\tau \in \chi(0)$  be a loop characteristic cell. For  $x \in \mathcal{N}(\tau; \varepsilon)$ ,*

$$\mathcal{R}(Z, \varepsilon) = \prod_{d=1}^{n+1} \mathcal{R}^d(Z, \varepsilon; \tau).$$

It is important to note that if  $\mathcal{R}^d(Z, \varepsilon; \tau)$  has an equilibrium, the equilibrium may not lie in  $\mathcal{N}^d(\tau; \varepsilon)$  so there may not be a corresponding equilibrium of  $\mathcal{R}(Z, \varepsilon)$ . A characterization of when an equilibrium of the switching system  $\mathcal{R}^d(Z, 0; \tau)$  corresponds to an equilibrium of  $\text{SWITCH}(Z)$  is given in [Duncan *et al.*, 2021]. It is straightforward to generalize these conditions to ramp systems, but for brevity we do not do so here. For the purpose of this paper we need only the following definitions which extend similar definitions for switching systems given in [Duncan *et al.*, 2021].

**Definition 5.2.** Given a loop characteristic cell  $\tau$  with permutation  $\rho = \rho^\tau$ , the *cone*  $\mathbf{C}(\kappa; \tau)$  rooted in  $\tau$  and induced by a cell  $\kappa \in \mathcal{N}(\tau)$  is defined by its  $N$  projections. For a regular direction,  $r$ , of  $\tau$

$$\pi_r(\mathbf{C}(\kappa; \tau)) := \pi_r(\tau).$$

For a singular direction,  $s \in \text{sd}(\tau)$ ,

$$\pi_s(\mathbf{C}(\kappa; \tau)) := \begin{cases} \{\theta_{\rho(s)s}\}, & \text{if } \pi_s(\kappa) = \{\theta_{\rho(s)s}\} \\ (\theta_{\rho(s)s}, \infty), & \text{if } \pi_s(\kappa) = (\theta_{\rho(s)s}, \theta_{\rho_+(s)s}) \\ (0, \theta_{\rho(s)s}), & \text{if } \pi_s(\kappa) = (\theta_{\rho_-(s)s}, \theta_{\rho(s)s}). \end{cases}$$

The *perturbed cone*  $\mathbf{C}(\kappa; \tau, \varepsilon)$  is defined by  $\tilde{\phi}^\varepsilon(\mathbf{C}(\kappa; \tau))$  where  $\tilde{\phi}^\varepsilon$  is defined in Section 3.1. For  $\sigma \in \mathcal{N}^d(\tau)$  define a  $d$ -cone in  $\mathbf{R}_+^{\ell_d}$  by

$$\mathbf{C}^d(\sigma; \tau, \varepsilon) := \prod_{j=s_d+1}^{s_d+\ell_d} \pi_j(\mathbf{C}(\sigma; \tau, \varepsilon)).$$

The perturbed cones  $\{\mathbf{C}^d(\sigma; \tau, \varepsilon) \mid \sigma \in \mathcal{N}(\tau)\}$ , consist of all the cells in the ramp complex of  $\mathcal{R}^d(Z, \varepsilon; \tau)$  except for the cells which lie on the boundary of  $\mathbf{R}_+^{\ell_d}$ .

**Definition 5.3.** Given a perturbation parameter  $\varepsilon$  and loop characteristic cell  $\tau$ , the  $d$ -*candidate equilibrium cells* of  $(\tau, \varepsilon)$  are defined by

$$\text{Eq}^d(\tau; \varepsilon) := \{\sigma^d \mid \sigma \in \mathcal{N}(\tau) \text{ and } \mathbf{C}^d(\sigma; \tau, \varepsilon) \text{ is an equilibrium cell of } \mathcal{R}^d(Z, \varepsilon; \tau)\}.$$

The *candidate equilibrium cells* of  $(\tau, \varepsilon)$  are  $\text{Eq}(\tau; \varepsilon) := \prod_{d=1}^{n+1} \text{Eq}^d$ .

It is clear that if  $\sigma \in \mathcal{N}(\tau; \varepsilon)$  is an  $\mathcal{R}$ -equilibrium cell then  $\sigma \in \text{Eq}(\tau; \varepsilon)$ . This is proven for  $\varepsilon = 0$  in [Duncan *et al.*, 2021].

## 5.2. Stability of Equilibria

The decomposition in Theorem 3 implies that in  $\mathcal{R}(Z, \varepsilon)$ , the stability of a  $\mathcal{R}(Z, \varepsilon)$  equilibrium  $x \in \mathcal{N}(\tau)$  is determined by the stability of  $x^d$  as an equilibrium of  $\mathcal{R}^d(Z, \varepsilon; \tau)$  for  $d = 1, \dots, n+1$ . We formally state this observation as a theorem after the following definition.

**Definition 5.4.** An equilibrium  $x$  of  $\mathcal{R}(Z, \varepsilon)$  is  $d$ -*stable* if  $x^d$  is stable as an equilibrium of  $\mathcal{R}^d(Z, \varepsilon; \tau)$  and  $d$ -*unstable* otherwise. If  $\mathcal{R}^d(Z, \varepsilon; \tau)$  undergoes a bifurcation at  $x^d$  then we say  $\mathcal{R}(Z, \varepsilon)$  has a  $d$ -bifurcation at  $x$ .

**Theorem 4.** Let  $Z \sim_W (Z, \varepsilon)$  and  $x \in \mathcal{N}(\tau; \varepsilon)$  be an equilibrium of  $\mathcal{R}(Z, \varepsilon)$ . Then  $x$  is stable if and only if  $x$  is  $d$ -stable for each  $d$ .

Proposition 1 now immediately generalizes.

**Theorem 5.** Let  $Z \sim_S (Z, \varepsilon)$  and  $\kappa \in \mathcal{N}(\tau)$  be an equilibrium cell. If  $c_d$  is a positive cycle then the equilibrium of  $\mathcal{R}(Z, \varepsilon)$  in  $\kappa(\varepsilon)$  is  $d$ -stable if, and only if,  $\kappa^d$  is a regular cell of  $\mathcal{R}^d(Z, \varepsilon)$ .

## 5.3. Border Crossing Bifurcations

Extending Propositions 2 and 3 to a general network is straightforward once we understand the values of  $L_{j(j-1)}^d$  and  $U_{j(j-1)}^d$  corresponding to the CFS  $\mathcal{R}^d(Z, \varepsilon; \tau)$  in the decomposition of  $\mathcal{R}(Z, \varepsilon)$  at loop characteristic cell  $\tau$ . To do so, we introduce the concept of a *neighbor* of a cell. An example of neighbors in the positive toggle switch can be found in Figure 1.

**Definition 5.5.** Let  $\tau \in \chi(\varepsilon)$  be a cell in the ramp complex and  $j \in V$ . If  $j$  is a singular direction  $j \in \text{sd}(\tau)$  let  $\pi_j(\tau) = \{\zeta_{i_j j}\}$  and  $\zeta_{i_1^+ j} < \zeta_{i_j j} < \zeta_{i_2^+ j}$  be consecutive thresholds. The *left  $k$ -neighbor* of the cell  $\tau$  is a cell  $\tau_k^-$ , defined by

$$\pi_j(\tau_k^-) := \begin{cases} \pi_j(\tau), & j \neq k \\ (\zeta_{i_1^+ j}, \zeta_{i_j j}), & j = k, k \in \text{sd}(\tau) \\ \inf(\pi_j(\tau)), & j = k, k \notin \text{sd}(\tau). \end{cases}$$

Similarly, the *right  $k$ -neighbor*,  $\tau_k^+$ , is defined by

$$\pi_j(\tau_k^+) := \begin{cases} \pi_j(\tau), & j \neq k \\ (\zeta_{i_j j}, \zeta_{i_2^+ j}), & j = k, k \in \text{sd}(\tau) \\ \sup(\pi_j(\tau)), & j = k, k \notin \text{sd}(\tau). \end{cases}$$

A  *$k$ -neighbor* of  $\tau$  is either a left or right  $k$ -neighbor of  $\tau$ . A *neighbor* of  $\tau$  is any  $k$ -neighbor.

Note that if  $j$  is a singular direction of  $\tau \in \chi(0)$ , then  $j$  is a regular direction of  $\tau_j^\pm$ . On the other hand, every singular direction  $s \in \text{sd}(\tau) \setminus \{j\}$  is a singular direction of  $\tau_j^\pm$ . Suppose  $\tau$  is a loop characteristic cell, let  $\rho = \rho^\tau$  and  $j' = \rho(j)$ . Since  $j$  is the unique direction which maps to  $j'$  under  $\rho$ , i.e.  $\rho^{-1}(\{j'\}) = \{j\}$ , Lemma 1 implies that  $\Lambda_{\rho(j)}(\tau_j^\pm)$  is well defined. We state this observation as the following lemma, which was first stated in [Duncan *et al.*, 2021].

**Lemma 2.** [Duncan *et al.*, 2021]. *Let  $\tau \in \chi(0)$  be a loop characteristic cell. If  $s$  is a singular direction of  $\tau$  then  $\Lambda_{\rho(s)}(\tau_s^\pm)$  is well defined.*

Lemmas 1 and 2 now imply that  $\Lambda_{\rho(j)}^\dagger(\cdot; \tau)$  can only take two possible values:  $\Lambda_{\rho(j)}^\dagger(\tau_j^-; \tau)$  and  $\Lambda_{\rho(j)}^\dagger(\tau_j^+; \tau)$ .

So, if  $\mathbf{RN}^d(\tau)$  is treated as an independent cyclic feedback network with switching parameter  $Z^d = (L^d, U^d, \theta^d, \Gamma^d)$ , then since we have assumed  $\mathbf{RN}^d(\tau)$  has activating edges except perhaps for  $(s_d + \ell_d, 1)$ , for a positive cyclic system ( $\text{sgn}(c_d) = 1$ )

$$L_{c_d(j)j}^d = \Lambda_{c_d(j)}(\tau_j^-), \quad \text{and} \quad U_{c_d(j)j}^d = \Lambda_{c_d(j)}(\tau_j^+)$$

for  $s_d + 1 \leq j \leq s_d + \ell_d$ . For a negative CFS ( $\text{sgn}(c_d) = -1$ ) the above equations hold for  $s_d + 1 \leq j < s_d + \ell_d$  and for the last equation we have

$$L_{(s_d+1)(s_d+\ell_d)}^d = \Lambda_{s_d+1}(\tau_{(s_d+\ell_d)}^+), \quad \text{and} \quad U_{(s_d+1)(s_d+\ell_d)}^d = \Lambda_{s_d+1}(\tau_{(s_d+\ell_d)}^-).$$

Applying Proposition 2 to  $\mathcal{R}^d(Z, \varepsilon; \tau)$  now yields an explicit condition for a  $d$ -saddle node when  $c_d$  is a positive cycle.

**Theorem 6.** *Let  $Z \sim_W (Z, \varepsilon)$  and let  $\tau$  be a loop characteristic cell with  $\rho^\tau|_{\text{sd}(\tau)} = (c_1, \dots, c_n)$ . Suppose  $\mathcal{R}(Z, \varepsilon)$  has a cycle in  $\mathcal{N}(\tau; \varepsilon)$ . Suppose  $c_d$  is a positive cycle and the ramp parameter  $(Z, \varepsilon^0)$  satisfies one of the following conditions*

- (1)  $\gamma_j(\theta_{c_d(j)j} - \varepsilon_{c_d(j)j}^0) = \Lambda_j(\tau_{c_d^{-1}(j)}^-)$  and  $\gamma_j(\theta_{c_d(j)j} + \varepsilon_{c_d(j)j}^0) < \Lambda_j(\tau_{c_d^{-1}(j)}^+)$  or
- (2)  $\gamma_j(\theta_{c_d(j)j} + \varepsilon_{c_d(j)j}^0) = \Lambda_j(\tau_{c_d^{-1}(j)}^+)$  and  $\gamma_j(\theta_{c_d(j)j} - \varepsilon_{c_d(j)j}^0) > \Lambda_j(\tau_{c_d^{-1}(j)}^-)$

for each  $j \in \{s_d + 1, \dots, \text{sd} + \ell_d\}$ . If  $\varepsilon < \varepsilon^0$  then  $\mathcal{R}(Z, \varepsilon; \tau)$  has two  $d$ -stable candidate equilibrium cells and one  $d$ -unstable candidate equilibrium cell. If  $\varepsilon > \varepsilon^0$  then  $\mathcal{R}(Z, \varepsilon; \tau)$  has one  $d$ -stable candidate equilibrium cell when  $\varepsilon - \varepsilon^0$  is sufficiently small. That is,  $\mathcal{R}(Z, \varepsilon)$  has a  $d$ -saddle node bifurcation at  $\varepsilon = \varepsilon^0$ .

Applying Proposition 3, yields a condition for a  $d$ -pitchfork when  $c_d$  is a positive cycle.

**Theorem 7.** Let  $(Z, \varepsilon) \sim_W (Z, 0)$  and  $\tau$  be a loop characteristic cell with  $\rho^\tau|_{\text{sd}(\tau)} = (c_1, \dots, c_n)$ . Suppose  $c_d$  is a positive cycle and the ramp parameter  $(Z, \varepsilon^0)$  satisfies

$$\gamma_j(\theta_{c_d(j)j} - \varepsilon_{c_d(j)j}^0) = \Lambda_j(\tau_{c_d(j)-1}^-) \quad \text{and} \quad \gamma_j(\theta_{c_d(j)j} + \varepsilon_{c_d(j)j}^0) = \Lambda_j(\tau_{c_d(j)-1}^+).$$

Then for  $\varepsilon < \varepsilon^0$ ,  $\mathcal{R}(Z, \varepsilon; \tau)$  has two  $d$ -stable candidate equilibrium cells and one  $d$ -unstable candidate equilibrium cell. If  $\varepsilon > \varepsilon^0$  then  $\mathcal{R}(Z, \varepsilon; \tau)$  has one  $d$ -stable candidate equilibrium cell. That is,  $\mathcal{R}(Z, \varepsilon)$  has a  $d$ -pitchfork bifurcation at  $\varepsilon = \varepsilon^0$ .

To extend Theorem 2, we define the product of the slopes of the ramp functions appearing in  $\mathcal{R}^d(Z, \varepsilon; \tau)$  for a given loop characteristic cell  $\tau$ . Defining  $\rho = \rho^\tau$  this product is given by

$$M^d(\varepsilon; \tau) := \prod_{j=s_d+1}^{s_d+\ell_d} \frac{\partial}{\partial x_{\rho(j)}} R_j(x; \varepsilon), \quad x \in \tau.$$

**Theorem 8.** Let **RN** be a regulatory network and consider a parameterization of ramp parameters  $(Z, \varepsilon)$  by a parameter  $s$ ,  $(Z(s), \varepsilon(s))$  with  $\varepsilon(s) = 0$  and  $Z(0) \sim_W (Z(s), \varepsilon(s))$ . Let  $\tau$  be a singular loop characteristic cell and suppose  $\mathcal{R}(Z(s), \varepsilon(s))$  has a non-degenerate border crossing  $d$ -bifurcation at  $x \in \mathcal{N}(\tau; \varepsilon)$  when  $s = s_0$ .

- (1) If  $x^d \notin \partial\tau^d(\varepsilon(s_0))$  then the bifurcation is persistent and stability does not change.
- (2) If  $x^d \in \partial\tau^d(\varepsilon(s_0))$  and  $\text{sgn}(c_d) = 1$ , then the bifurcation is a non-smooth saddle node if  $M^d(\varepsilon(s_0)) > \prod_{j=s_d+1}^{s_d+\ell_d} \gamma_j$  and a stability preserving persistent bifurcation if  $M^d(\varepsilon(s_0)) < \prod_{j=s_d+1}^{s_d+\ell_d} \gamma_j$ .
- (3) If  $x^d \in \partial\tau^d(\varepsilon(s_0))$ ,  $\Gamma(s_0) = I$ , and  $\text{sgn}(c_d) = -1$ , then the bifurcation is a stability changing persistent bifurcation if  $N > 2$  and  $M^d(\varepsilon(s_0)) > \sec(\pi/\ell_d)^{\ell_d}$  and a stability preserving persistent bifurcation if  $N \leq 2$  or  $M^d(\varepsilon(s_0)) < \sec(\pi/\ell_d)^{\ell_d}$ .

To see the significance of this theorem, we make a similar observation as the one following Theorem 2. Theorem 8 implies that if weak equivalence holds, detection of steady state bifurcations in  $\mathcal{R}(Z, \varepsilon)$ , requires tracking the (possibly virtual) equilibrium in each loop characteristic cell  $\tau$  but not any other equilibria. If the equilibrium is not virtual, then  $M^d(\varepsilon)$  for each cycle  $c_d$  in the cycle decomposition of  $\rho^\tau$  needs to be tracked as well to detect smooth bifurcations. Given a ramp parameterization of the form  $(Z, \varepsilon(s))$  where  $\varepsilon(0) = 0$  and  $\varepsilon(s)$  is monotonically increasing function, we can therefore use Theorem 8 to determine the minimum value of  $s$  where the number or stability of  $\mathcal{R}(Z, \varepsilon(s))$  changes, provided that this change happens while  $Z \sim_W (Z(s), \varepsilon(s))$ .

## 6. Preserving Equilibria while Minimizing Slopes

Our goal in this section is to understand what is the minimal slope of ramp functions  $R_{ij}$  at which the collection of equilibria and their stability for the ramp system  $\mathcal{R}(Z, \varepsilon)$  is the same as the collection and stability of equilibria, both regular and SSPs, of the switching system **SWITCH**( $Z$ ). As observed in Section 5, given a parameterization of ramp parameters  $(Z, \varepsilon(s))$  so that  $\varepsilon(0) = 0$  and  $\varepsilon(s)$  monotone increasing, Theorem 8 can be used to find the value of  $s$  which attains the minimal slope of the linear portion of the ramp functions for this parameterization. In this section we seek to find the minimal slope independent of any parameterization.

Recall that the slope of the ramp function  $R_{ij}$  is denoted by  $m_{ij}(\varepsilon)$ . Then we seek to find

$$m^* := \max_{j=1, \dots, N} m_{\min}(Z, j) \quad \text{where} \quad (9)$$

$$m_{\min}(Z, j) := \min_{\varepsilon \in \mathcal{E}(Z)} \max_{i \in \mathbf{T}(j)} \{m_{ij}(\varepsilon_{ij})\} \quad (10)$$

and the set

$$\mathcal{E}(Z) = \{\varepsilon \mid Z \sim_S (Z, \varepsilon)\}$$

is the collection of all  $\varepsilon$  for which the parameter  $(Z, \varepsilon)$  is strongly equivalent to  $Z$ . By Theorem 1 and Proposition 1,  $m^*$  is an upper bound on the minimal slope of all ramp functions such that the stability

of all equilibria are maintained. The value  $m^*$  is this minimal slope unless there is an equilibrium within a loop characteristic cell  $\tau$  such that  $\mathcal{R}(Z, \varepsilon)$  decomposes into exclusively negative CFSs and a diagonal system. Such an equilibrium may be stable for  $\mathcal{R}(Z, \varepsilon)$  and unstable for  $\text{SWITCH}(Z)$  even when the slopes of the corresponding ramp functions are larger than  $m^*$ . If  $\Gamma = I$ , stability of these equilibria of  $\mathcal{R}(Z, \varepsilon)$  at  $m^*$  can be determined using Proposition 4.11 of [Duncan *et al.*, 2021]. Note that this optimization problem assumes that the parameter  $Z$  is fixed and seeks to optimize selection of  $\varepsilon_{ij}$ .

After we address this problem we assume that the values of  $L_{ij}, U_{ij}$  within the parameter  $Z$  are fixed, but we allow the set of threshold values to change. In this situation, the solution of the optimization problem (9) depends on the collection  $\{\theta_{ij}\}$ ; thus  $m^* = m^*(\{\theta_{ij}\})$ . We then discuss minimization of  $m^*$  over all such choices of thresholds.

### 6.1. Minimizing Slope for Fixed Parameter $Z$

This subsection solves the problem of computing  $m^*$  when  $Z = (L, U, \theta, \Gamma)$  is fixed by providing an explicit choice of  $\varepsilon$  which achieves  $m^*$ . Our strategy is to divide the optimization problem (9) into two parts. First we split the set  $\mathcal{E}(Z)$  into sets of  $\varepsilon$  that correspond to each variable  $x_j$

$$\mathcal{E}(Z) = \bigoplus_{j=1}^N \mathcal{E}^j(Z)$$

where

$$\mathcal{E}^j(Z) := \{\varepsilon \in \mathcal{E}(Z) \mid \varepsilon_{ik} = 0 \text{ if } k \neq j\}$$

is the set of  $\varepsilon \in \mathcal{E}(Z)$  such that for a fixed  $j$  only the entries  $\varepsilon_{ij}$ ,  $i \in V$ , are non-zero. We can think of a perturbation parameter  $\varepsilon$  as an  $N \times N$  matrix where non-zero elements are in the positions  $ij$  when there is a network edge from node  $j$  to node  $i$ . Then  $\mathcal{E}^j(Z)$  contain only those matrices  $\varepsilon$  where only the  $j$ th column of  $\varepsilon$  is non-zero.

First, in Proposition 4 for each  $j$  we find an  $\varepsilon^j \in \overline{\mathcal{E}^j(Z)}$  which achieves  $m_{\min}(Z, j)$ . Then in Theorem 9 we combine the optimal  $\varepsilon^j$  to find the minimizer  $\varepsilon$ .

We further subdivide the problem of finding  $\varepsilon^j$  by splitting the set  $\mathcal{E}^j(Z)$  further and optimizing over each subset in this decomposition. Recall that  $\omega_j$  is the  $\Lambda_j$ -evaluation function and  $\text{In}_j$  is the set of input combinations for the  $j$ th node (Definition 3.7). The  $\omega_j$  depends on the fixed parameter  $Z$ .

#### Definition 6.1.

Given parameter  $Z$ , we write the range of the  $\Lambda_j$ -evaluation function  $\omega_j$  as  $\omega_j(\text{In}_j) = \{w_1, \dots, w_{n-1}\}$  with  $0 =: w_0 < w_1 < \dots < w_{n-1} < w_n := \infty$  and define

$$W_j := \omega_j(\text{In}_j) \cup \{0, \infty\}. \quad (11)$$

Let

$$B^{j,p}(\theta) := \{i \in \mathbf{T}(j) \mid w_{p-1} < \gamma_j \theta_{ij} \leq w_p\}$$

be the set of indices of target nodes of node  $j$ , for which the thresholds  $\theta_{ij}$  associated to edges  $(j, i)$ , weighted by  $\gamma_j$ , fall between  $w_{p-1}$  and  $w_p$ , and

$$\mathcal{E}^{j,p}(Z) := \{\varepsilon \in \mathcal{E}^j(Z) \mid \varepsilon_{ij} = 0 \text{ if } i \notin B^{j,p}(\theta)\}$$

be the set of  $\varepsilon$  where the only nonzero entries are those that correspond to thresholds indexed by  $B^{j,p}(\theta)$ . Then we can decompose  $\mathcal{E}^j(Z)$  as a sum

$$\mathcal{E}^j(Z) = \bigoplus_{p=1}^n \mathcal{E}^{j,p}(Z).$$

In Lemma 3, we find an optimal choice of  $\varepsilon^{j,p} \in \overline{\mathcal{E}^{j,p}(Z)}$ . An optimal choice of  $\varepsilon^j \in \overline{\mathcal{E}^j(Z)}$  and then of  $\varepsilon \in \overline{\mathcal{E}(Z)}$  will then follow from this result. The idea of how to choose  $\varepsilon^{j,p}$  is simple but the notation

is complicated by the generality of the result. The main insight, which we justify in the proof, is that an optimal  $\varepsilon^{j,p}$  can always be chosen so that the relevant slopes  $m_{ij}$  are identical. Once we have assumed that the slopes are equal, the multi-variable optimization problem becomes a single variable problem.

To state the lemma, we define the difference between the values realized by the switching function  $\sigma_{ij}$  to be  $\Delta_{ij} := U_{ij} - L_{ij}$ .

**Lemma 3.** *Let  $Z$  be a switching parameter and  $B^{j,p}(\theta) = \{i_1, \dots, i_k\}$  with  $\theta_{i_{q-1}j} < \theta_{i_qj}$ . Let*

$$D_\ell(Z) := \frac{\gamma_j \theta_{i_{1j}} - w_{p-1}}{\gamma_j \Delta_{i_{1j}}}, \quad D_{mid}(Z) = \min_{q>1} \frac{\theta_{i_{qj}} - \theta_{i_{q-1}j}}{\Delta_{i_{q-1}j} + \Delta_{i_{qj}}}, \quad D_r(Z) := \frac{w_p - \gamma_j \theta_{i_{kj}}}{\gamma_j \Delta_{i_{kj}}},$$

and

$$D(Z) = \begin{cases} \min\{D_{mid}(Z), D_r(Z)\} & p = 1 \\ \min\{D_\ell(Z), D_{mid}(Z)\} & p = n \\ \min\{D_\ell(Z), D_{mid}(Z), D_r(Z)\} & \text{otherwise} \end{cases} \quad (12)$$

Let  $\varepsilon^{j,p} \in \overline{\mathcal{E}^{j,p}(Z)}$  be such that its non-zero elements are given by

$$\varepsilon_{ij}^{j,p} = \Delta_{ij} D(Z). \quad (13)$$

Then

$$\min_{\varepsilon \in \overline{\mathcal{E}^{j,p}(Z)}} \max_{i \in B^{j,p}(\theta)} \{m_{ij}(\varepsilon_{ij})\}. \quad (14)$$

is achieved at  $\varepsilon^{j,p}$ .

*Proof.* To simplify notation let  $\varepsilon = \varepsilon^{j,p}$ . By the definition of  $D(Z)$  and  $\varepsilon$ , for all  $q > 1$  the distances between the consecutive thresholds between  $w_{p-1}$  and  $w_p$  satisfy

$$\begin{aligned} \theta_{i_{qj}} - \varepsilon_{i_{qj}} - (\theta_{i_{q-1}j} + \varepsilon_{i_{q-1}j}) &= \theta_{i_{qj}} - \Delta_{i_{qj}} D(Z) - (\theta_{i_{q-1}j} + \Delta_{i_{q-1}j} D(Z)) \\ &= \theta_{i_{qj}} - \theta_{i_{q-1}j} - (\Delta_{i_{qj}} + \Delta_{i_{q-1}j}) D(Z) \\ &\geq \theta_{i_{qj}} - \theta_{i_{q-1}j} - (\theta_{i_{qj}} - \theta_{i_{q-1}j}) = 0. \end{aligned}$$

Note that the last line holds with equality when  $D(Z) = D_{mid}(Z)$ . Now we compute the distance between  $w_{p-1}$  and the first threshold in  $B^{j,p}(\theta)$ , which only makes sense when  $p \neq 1$

$$\begin{aligned} \gamma_j(\theta_{i_{1j}} - \varepsilon_{i_{1j}}) - w_{p-1} &= \gamma_j(\theta_{i_{1j}} - \Delta_{i_{1j}} D(Z)) - w_{p-1} \\ &= \gamma_j \theta_{i_{1j}} - w_{p-1} - \gamma_j \Delta_{i_{1j}} D(Z) \\ &\geq \gamma_j \theta_{i_{1j}} - w_{p-1} - (\gamma_j \theta_{i_{1j}} - w_{p-1}) = 0 \end{aligned}$$

and the last line holds with equality when  $D(Z) = D_\ell(Z)$ . Finally, we compute the distance between the last threshold in  $B^{j,p}(\theta)$  and  $w_p$  which only makes sense when  $p \neq n$ .

$$\begin{aligned} w_p - \gamma_j(\theta_{i_{kj}} + \varepsilon_{i_{kj}}) &= w_p - \gamma_j \theta_{i_{kj}} - \gamma_j \Delta_{i_{kj}} D(Z) \\ &\geq w_p - \gamma_j \theta_{i_{kj}} - (w_p - \gamma_j \theta_{i_{kj}}) = 0 \end{aligned}$$

and the last line holds with equality when  $D(Z) = D_r(Z)$ . We have shown

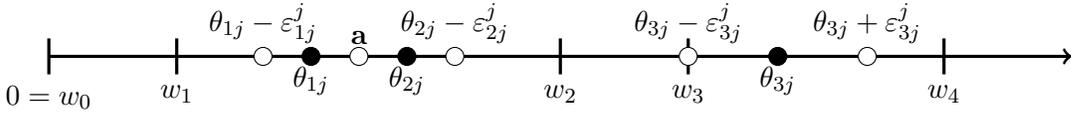
$$\begin{aligned} w_{p-1} &\leq \gamma_j(\theta_{i_{1j}} - \varepsilon_{i_{1j}}), \quad \text{if } p \neq 1 \text{ and} \\ \theta_{i_{q-1}j} - \varepsilon_{i_{q-1}j} &\leq \theta_{i_{qj}} - \varepsilon_{i_{qj}}, \quad \text{for all } q > 1, \text{ and} \\ \theta_{i_{kj}} - \varepsilon_{i_{kj}} &\leq w_p, \quad \text{if } p \neq n \end{aligned} \quad (15)$$

and that at least one of the above equations holds with equality. If  $\varepsilon'_{ij} < \varepsilon_{ij}$  whenever  $\varepsilon_{ij} \neq 0$ , then ' $\leq$ ' is replaced with ' $<$ ' in each of the above equations. This implies  $(Z, \varepsilon') \sim_S Z$  so that  $\varepsilon' \in \mathcal{E}^{j,p}(Z)$ . We can therefore construct a sequence of  $\varepsilon^\ell$  such that  $\varepsilon^\ell \in \mathcal{E}^{j,p}(Z)$  for each  $\ell$  and  $\varepsilon^\ell \rightarrow \varepsilon$  as  $\ell \rightarrow \infty$  which shows  $\varepsilon \in \overline{\mathcal{E}^{j,p}(Z)}$ .

Now we show that (14) is achieved at  $\varepsilon$ . First, we note that for each  $i \in B^{j,p}(\theta)$ ,

$$m_{ij}(\varepsilon_{ij}) = \frac{\Delta_{ij}}{2\varepsilon_{ij}} = \frac{\Delta_{ij}}{2\Delta_{ij}D(Z)} = \frac{1}{2D(Z)}$$

so that at  $\varepsilon$ , all the slopes are identical. Now suppose (14) is achieved at  $\varepsilon' \in \overline{\mathcal{E}^{j,p}(Z)}$ . We must have  $\varepsilon' \geq \varepsilon$  as  $m_{ij}$  is a decreasing function of  $\varepsilon_{ij}$ . If (14) is not achieved at  $\varepsilon$ , then  $\varepsilon'_{ij} > \varepsilon_{ij}$  for all  $i \in B^{j,p}(\theta)$  because all the slopes are identical at  $\varepsilon$ . But one of the equations in (15) is satisfied with equality by  $\varepsilon$ . Therefore, if we replace  $\varepsilon$  with  $\varepsilon'$  in (15), one of the ' $\leq$ ' must be replaced with a '>'. Indeed this is true for all  $\varepsilon''$  with  $\varepsilon < \varepsilon'' \leq \varepsilon'$  so that  $(Z, \varepsilon'')$  is not strongly equivalent to  $Z$ . This implies there is an open neighborhood of  $\varepsilon'$  which does not intersect  $\mathcal{E}^{j,p}(Z)$  and  $\varepsilon' \notin \overline{\mathcal{E}^{j,p}(Z)}$ , a contradiction. ■



**Fig. 3. Example of  $\varepsilon^j$  for a node  $j$  with two sources and three targets.** Since  $j$  has two sources,  $\Lambda_j$  takes 4 values and  $W_j = \{0 = w_0 < w_1 < w_2 < w_3 < w_4 < w_5 = \infty\}$ . The vertical lines indicate the values of  $w_0, \dots, w_4$ . We assume  $\gamma_j = 1$  and  $\mathbf{T}(j) = \{1, 2, 3\}$  with  $\theta_{1j} < \theta_{2j} < \theta_{3j}$ . The sets  $B^{j,1} = \emptyset$ ,  $B^{j,2} = \{1, 2\}$ ,  $B^{j,3} = \emptyset$ ,  $B^{j,4} = \{3\}$ , and  $B^{j,5} = \emptyset$  so that  $\mathcal{E}^{j,1} = \mathcal{E}^{j,3} = \mathcal{E}^{j,5} = \{0\}$ . The filled circles indicate the values of the thresholds. The unfilled circles indicate the values of  $\theta_{ij} \pm \varepsilon_{ij}$  for the optimal value of  $\varepsilon^j = \varepsilon^{j,2} + \varepsilon^{j,4}$  that is chosen as in Proposition 4. In particular,  $\varepsilon^{j,2} \in \overline{\mathcal{E}^{j,2}}$  is chosen so that  $\theta_{1j} + \varepsilon_{1j}^{j,2} = \theta_{2j} - \varepsilon_{2j}^{j,2}$  at the unfilled circle labeled **a**. All remaining entries of  $\varepsilon^{j,2}$  are zero. The optimal value  $\varepsilon^{j,4} \in \overline{\mathcal{E}^{j,4}}$  is achieved when  $\theta_{3j} - \varepsilon_{3j}^{j,4} = w_3$ . All other entries of  $\varepsilon^{j,4}$  are zero.

See Figure 3 for an example of  $\varepsilon^{j,p}$  for each  $p$  and a node  $j$  with two sources and three targets. Note that for distinct choices of  $p_1$  and  $p_2$ , any entry of  $\varepsilon^{j,p_1}$  is zero when the corresponding entry in  $\varepsilon^{j,p_2}$  is non-zero. To find a value  $\varepsilon^j$  which achieves  $m_{\min}(Z, j)$ , this structure allows us to sum over the values  $\varepsilon^{j,p}$ . Figure 3 indicates the value of  $\varepsilon^j$  as defined in the following proposition.

**Proposition 4.** *Let  $Z$  be a regular switching parameter and  $j \in V$ . Let  $\varepsilon^{j,p} \in \overline{\mathcal{E}^{j,p}(Z)}$  be defined as in Lemma 3. Then  $m_{\min}(Z, j)$  is achieved at  $\varepsilon^j \in \overline{\mathcal{E}^j(Z)}$  where*

$$\varepsilon^j = \sum_{p=1}^n \varepsilon^{j,p}.$$

*Proof.* For  $i_0 \notin B^{j,p}(\theta)$ ,  $\max_{i \in B^{j,p}(\theta)} \{m_{ij}(\varepsilon_{ij})\}$  is independent of  $\varepsilon_{i_0j}$ . Therefore, by Lemma 3, for each  $p$ ,

$$\min_{\varepsilon \in \overline{\mathcal{E}^{j,p}(Z)}} \max_{i \in B^{j,p}(\theta)} \{m_{ij}(\varepsilon_{ij})\}$$

is achieved at  $\varepsilon^j$ . So, if  $\varepsilon' \in \overline{\mathcal{E}^j(Z)}$ ,

$$\max_{i \in B^{j,p}(\theta)} \{m_{ij}(\varepsilon'_{ij})\} \geq \max_{i \in B^{j,p}(\theta)} \{m_{ij}(\varepsilon^j_{ij})\}.$$

Since  $\mathbf{T}(j) = \bigcup_{p=1}^n B^{j,p}(\theta)$  we have

$$\max_{i \in \mathbf{T}(j)} \{m_{ij}(\varepsilon'_{ij})\} \geq \max_{i \in \mathbf{T}(j)} \{m_{ij}(\varepsilon^j_{ij})\}.$$

■

Note that for distinct choices of  $j_1, j_2 \in V$ , an entry of  $\varepsilon^{j_1}$  is zero whenever the corresponding entry of  $\varepsilon^{j_2}$  is non-zero. Therefore to construct a value of  $\varepsilon$  which achieves  $m^*$ , we sum over the  $\varepsilon^j$ .

**Theorem 9.** *Let  $Z$  be a regular switching parameter. For each  $j \in V$  let  $\varepsilon^j$  be defined as in Proposition 4. Then  $m^*$  is achieved at  $\varepsilon \in \mathcal{E}(Z)$  defined by*

$$\varepsilon = \sum_{j=1}^N \varepsilon^j.$$

*Proof.* For  $k \neq j$ ,  $\max_{i \in \mathbf{T}(j)} \{m_{ij}(\varepsilon_{ij})\}$  is independent of  $\varepsilon_{ik}$ . Therefore, by Proposition 4,  $\varepsilon$  attains  $m_{\min}(Z, j)$  for each  $j \in V$  so that  $m^*$  is achieved at  $\varepsilon$ . ■

## 6.2. Minimizing Slope for Fixed $L, U$ , and $\Gamma$

For each fixed arrangement of thresholds, the previous section constructed a collection  $\varepsilon$  that minimizes slopes. Here we further minimize the slopes over all possible arrangements of thresholds  $\theta$  within the fixed order given by  $Z$ . Specifically, let  $Z^0 = (L, U, \theta^0, \Gamma)$  be a fixed switching parameter and define

$$\begin{aligned} \Theta'(Z^0) &= \{\theta \mid ((L, U, \theta, \Gamma), 0) \sim_S (Z^0, 0)\} \quad \text{and} \\ Q(Z^0) &= \{(\theta, \varepsilon) \mid \theta \in \Theta'(Z^0), \varepsilon \in \mathcal{E}((L, U, \theta, \Gamma))\}. \end{aligned}$$

We solve

$$m^* := \max_{j=1, \dots, N} \inf_{(\theta, \varepsilon) \in \overline{Q(Z)}} \max_{i \in \mathbf{T}(j)} \{m_{ij}(\varepsilon_{ij})\}. \quad (16)$$

Typically the infimum is in fact a minimum for at least one node  $j = 1, \dots, N$ . In this case we provide an explicit choice of  $(\theta, \varepsilon) \in \overline{Q(Z)}$  which achieves (16). However, there is a case wherein the infimum is not achieved for any node. In this case, we provide a sequence  $(\theta^\ell, \varepsilon^\ell)$  so that the value of (16) is 0 in the limit  $\ell \rightarrow \infty$ .

As in the previous subsection, we divide the problem into parts. Define

$$Q^j(Z^0) := \{(\theta, \varepsilon) \in Q(Z^0) \mid \theta_{ik} = \theta_{ik}^0 \text{ if } k \neq j \text{ and } \varepsilon \in \mathcal{E}^j((L, U, \theta, \Gamma))\}.$$

We solve

$$\inf_{(\theta, \varepsilon) \in \overline{Q^j(Z^0)}} \max_{i \in \mathbf{T}(j)} \{m_{ij}(\varepsilon_{ij})\} \quad (17)$$

in Propositions 6 and 5. This is done by first partitioning the thresholds according to the set  $W_j$ , which was defined in Definition 6.1.

Define

$$Q^{j,p}(Z^0) := \{(\theta, \varepsilon) \in Q^j(Z^0) \mid \theta_{ij} = \theta_{ij}^0 \text{ if } i \notin B^{j,p}(\theta^0) \text{ and } \varepsilon \in \mathcal{E}^{j,p}((L, U, \theta, \Gamma))\},$$

where we fix all thresholds outside of the set  $B^{j,p}(\theta^0)$ . Most of the work lies in finding the optimal solution in the set  $Q^{j,p}(Z^0)$ , which is a joint optimization over thresholds indexed by  $B^{j,p}(\theta)$  and  $\varepsilon \in \mathcal{E}^{j,p}(Z^0)$

$$\inf_{(\theta, \varepsilon) \in \overline{Q^{j,p}(Z^0)}} \max_{i \in B^{j,p}(\theta)} \{m_{ij}(\varepsilon_{ij})\} \quad (18)$$

which we do in Lemmas 4 and 5.

To begin, we fix  $p < n$  and describe how to choose the thresholds which lie between  $w_{p-1}$  and  $w_p$  (i.e. in the set  $B^{j,p}(\theta^0)$ ) in the following definition. The definition is split based on whether  $p = 1$  or not because  $\theta_{ij} - \varepsilon_{ij} < 0 = w_0$  does not make strong equivalence fail whereas for  $p > 0$  the relation  $\theta_{ij} - \varepsilon_{ij} < w_p$  when  $\theta_{ij} > w_p$  does. The lemma that follows the definition proves that this choice is optimal. The case that  $p = n$  is another edge case which is handled differently from  $p = 1$  and is addressed later.

**Definition 6.2.** Let  $\theta$  be a threshold parameter,  $j \in V$ , and  $p < n$ . Let  $B^{j,p}(\theta) = \{i_1, \dots, i_k\}$  with  $\theta_{i_1 j} < \dots < \theta_{i_k j}$ .

(1) If  $p \neq 1$  we define

$$D^{j,p} = \frac{w_p - w_{p-1}}{2\gamma_j \sum_{\ell=1}^k \Delta_{i_{\ell j}}}.$$

and set the value of the first threshold  $\theta_{i_{1j}}$  so it satisfies

$$\gamma_j \theta_{i_{1j}} = w_{p-1} + \gamma_j \Delta_{i_{1j}} D^{j,p}.$$

(2) If  $p = 1$  we define

$$D^{j,p} = \frac{w_p}{\gamma_j \left( \Delta_{i_{1j}} + 2 \sum_{\ell=2}^k \Delta_{i_{\ell j}} \right)}$$

and set  $\theta_{i_{1j}} = 0$ .

We say  $\theta$  *maximally separates* the interval  $(w_{p-1}, w_p)$  if  $\theta$  satisfies (1) or (2) and for  $q > 1$

$$\theta_{i_{qj}} = \theta_{i_{q-1j}} + (\Delta_{i_{q-1j}} + \Delta_{i_{qj}}) D^{j,p}.$$

**Lemma 4.** *Let  $p < n$  and  $j \in V$ . Let  $(\theta^{j,p}, \varepsilon^{j,p}) \in \overline{Q^{j,p}(Z^0)}$  such that  $\theta^{j,p}$  maximally separates  $(w_{p-1}, w_p)$  and the non-zero entries of  $\varepsilon^{j,p}$  satisfy*

$$\varepsilon_{ij}^{j,p} = \Delta_{ij} D^{j,p}.$$

*Then the optimal solution of the problem (18) is achieved at  $(\theta^{j,p}, \varepsilon^{j,p})$ .*

*Proof.* To simplify notation, let  $(\theta, \varepsilon) = (\theta^{j,p}, \varepsilon^{j,p})$  and  $Z = (L, U, \theta, \Gamma)$ . We first consider the case  $p \neq 1$ . Since  $\theta$  maximally separates  $(w_{p-1}, w_p)$ , we have

$$\begin{aligned} \gamma_j (\theta_{i_{1j}} - \varepsilon_{i_{1j}}) &= \gamma_j \theta_{i_{1j}} - \gamma_j \Delta_{i_{1j}} D^{j,p} \\ &= w_{p-1} + \gamma_j \Delta_{i_{1j}} D^{j,p} - \gamma_j \Delta_{i_{1j}} D^{j,p} = w_{p-1}. \end{aligned}$$

and, for  $q > 1$ ,

$$\begin{aligned} \theta_{i_{qj}} - \varepsilon_{i_{qj}} &= \theta_{i_{q-1j}} + (\Delta_{i_{q-1j}} + \Delta_{i_{qj}}) D^{j,p} - \gamma_j \Delta_{i_{qj}} D^{j,p} \\ &= \theta_{i_{q-1j}} + \Delta_{i_{q-1j}} D^{j,p} = \theta_{i_{q-1j}} + \varepsilon_{i_{q-1j}}. \end{aligned}$$

It also follows from the inductive definition of maximal separation that

$$\gamma_j \theta_{i_{kj}} = w_{p-1} + \gamma_j \Delta_{i_{kj}} D^{j,p} + 2\gamma_j \sum_{q=1}^{k-1} \Delta_{i_{qj}} D^{j,p}$$

so that

$$\begin{aligned} \gamma_j (\theta_{i_{kj}} + \varepsilon_{i_{kj}}) &= \gamma_j \theta_{i_{kj}} + \gamma_j \Delta_{i_{kj}} D^{j,p} \\ &= w_{p-1} + \gamma_j \Delta_{i_{kj}} + 2\gamma_j \sum_{q=1}^{k-1} \Delta_{i_{qj}} D^{j,p} + \gamma_j \Delta_{i_{kj}} D^{j,p} \\ &= w_{p-1} + 2\gamma_j D^{j,p} \sum_{q=1}^k \Delta_{i_{qj}} \\ &= w_{p-1} + (w_p - w_{p-1}) = w_p. \end{aligned}$$

This shows that  $\theta \in \Theta'(Z^0)$  and  $\varepsilon \in \overline{\mathcal{E}^{j,p}(Z)}$ . Moreover, it shows that  $D^{j,p} = D(Z)$  where  $D(Z)$  is defined as in (12) so that by Lemma 3,

$$\min_{\varepsilon \in \overline{\mathcal{E}^{j,p}(Z)}} \max_{i \in B^{j,p}(\theta)} \{m_{ij}(\varepsilon_{ij})\}$$

is achieved at  $\varepsilon$ .

We now show that  $\theta$  is the optimal choice. Let  $(\theta', \varepsilon') \in \overline{Q^{j,p}(Z^0)}$  with  $\theta' \neq \theta$ . Let  $Z' = (L, U, \theta', \Gamma)$ . We may assume that  $\varepsilon' \in \overline{\mathcal{E}^{j,p}(Z')}$  is chosen according to Lemma 3. We claim

$$\begin{aligned} \gamma_j \theta'_{i_1^p j} - w_{p-1} &< \gamma_j \theta_{i_1^p j} - w_{p-1}, \text{ or} \\ \theta'_{i_q^p j} - \theta'_{i_{q-1}^p j} &< \theta_{i_q^p j} - \theta_{i_{q-1}^p j} \text{ for some } q > 1, \text{ or} \\ w_p - \gamma_j \theta'_{i_{k_p}^p j} &< w_p - \gamma_j \theta_{i_{k_p}^p j}. \end{aligned}$$

By a way of contradiction, suppose that this is not the case. Then

$$\begin{aligned} \gamma_j \theta'_{i_1^p j} - w_{p-1} &\geq \gamma_j \theta_{i_1^p j} - w_{p-1}, \text{ and} \\ \theta'_{i_q^p j} - \theta'_{i_{q-1}^p j} &\geq \theta_{i_q^p j} - \theta_{i_{q-1}^p j} \text{ for all } q > 1, \text{ and} \\ w_p - \gamma_j \theta'_{i_{k_p}^p j} &\geq w_p - \gamma_j \theta_{i_{k_p}^p j}. \end{aligned}$$

and at least one of the inequalities is strict as  $\theta'$  does not maximally separate  $(w_{p-1}, w_p)$ . Summing over each of the relations above then implies  $w_p - w_{p-1} > w_p - w_{p-1}$ , which is a contradiction. This proves the claim.

From the definition of  $D(Z)$ , the claim implies that  $D(Z') < D(Z) = D^{j,p}$  so that  $\varepsilon' < \varepsilon$ . Therefore

$$\max_{i \in B^{j,p}(\theta')} \{m_{ij}(\varepsilon')\} > \max_{i \in B^{j,p}(\theta)} \{m_{ij}(\varepsilon)\}.$$

For  $p = 1$ , we have to resolve a technical issue because  $\theta_{i_1 j} = 0$  implies  $Z$  is not regular so that there are no  $\varepsilon$  such that  $(Z, \varepsilon) \sim_S Z$ . To resolve this issue, we need to show that  $(\theta, \varepsilon)$  actually belongs to the set  $\overline{Q^{j,1}(Z^0)}$ . To do so, we describe a sequence  $(\theta^\ell, \varepsilon^\ell) \in Q^{j,1}(Z^0)$  which converges to  $(\theta, \varepsilon)$  as  $\ell \rightarrow \infty$ . For  $i \in B_j(w_0, w_1; \theta) \setminus \{i_1\}$  we define  $\theta_{i j}^\ell = \theta_{i j}$  and let  $\varepsilon_{i j}^\ell < \varepsilon_{i j}$  with  $\varepsilon_{i j}^\ell \rightarrow \varepsilon_{i j}$ . We then define  $\theta_{i_1 j}^\ell$  and  $\varepsilon_{i_1 j}^\ell$  so that  $\theta_{i_1 j}^\ell > 0$ ,  $\theta_{i_1 j}^\ell \rightarrow 0$ ,  $\varepsilon_{i_1 j}^\ell \rightarrow \varepsilon_{i_1 j}$ , and

$$0 < \theta_{i_1 j}^\ell + \varepsilon_{i_1 j}^\ell < \begin{cases} w_1, & B_j(w_0, w_1; \theta) = \{i_1\} \\ \theta_{i_2 j} - \varepsilon_{i_2 j}, & \text{otherwise} \end{cases}$$

for each  $\ell$ . Since  $\theta_{i j}^\ell - \varepsilon_{i j}^\ell > \theta_{i j}^\ell + \varepsilon_{i j}^\ell$  whenever  $\theta_{i j}^\ell > \theta_{i j}^\ell$  and  $\theta_{i j}^\ell + \varepsilon_{i j}^\ell < w_1$  for each  $i \in B_j(w_0, w_1; \theta^0)$ ,  $\theta^\ell \in \Theta'(Z^0)$  and  $\varepsilon^\ell \in \mathcal{E}^j((L, U, \theta^\ell, \Gamma), w_0, w_1)$ . Therefore,  $(\theta^\ell, \varepsilon^\ell) \in Q^{j,1}(Z^0)$  so that  $(\theta, \varepsilon) \in \overline{Q^{j,1}(Z^0)}$ .

The fact that  $(\theta, \varepsilon)$  is an optimal choice when  $p = 1$  follows now from a similar argument as the case  $p \neq 1$ . ■

We now address the case that  $p = n$ . In this case, the infimum is never achieved because there is no upper bound on  $\theta_{i j}$ . The thresholds can therefore be spaced arbitrarily far apart and the perturbations  $\varepsilon_{i j}$  can be made arbitrarily large so that the slopes  $m_{i j}$  can be made arbitrarily small. The following proposition formalizes this observation.

**Lemma 5.** *Let  $j \in V$  and  $p = n$ . Then*

$$\inf_{(\theta, \varepsilon) \in \overline{Q^{j,n}(Z^0)}} \max_{i \in B^{j,n}(\theta^0)} \{m_{i j}(\varepsilon_{i j})\} = 0.$$

*Proof.* Let  $B^{j,n}(\theta^0) = \{i_1, \dots, i_k\}$  with  $\theta_{i_1 j} < \dots < \theta_{i_k j}$ . Define a sequence  $(\theta^\ell, \varepsilon^\ell) \in Q^{j,n}(Z^0)$  so that for each  $q \in \{1, \dots, k\}$ ,

$$\gamma_j \theta_{i_q j}^\ell = w_{n-1} + q\ell \quad \text{and} \quad \gamma_j \varepsilon_{i_q j}^\ell = \frac{\ell}{4}.$$

Note that  $\gamma_j \theta_{i_q j}^\ell - \gamma_j \theta_{i_{q-1} j}^\ell = \ell$  and  $\gamma_j \theta_{i_1 j}^\ell - w_{n-1} = \ell$  so that  $(Z^\ell, 0) \sim_S (Z^0, 0)$ . We also have

$$\begin{aligned} \gamma_j(\theta_{i_q j} - \varepsilon_{i_q j}) - \gamma_j(\theta_{i_{q-1} j} + \varepsilon_{i_{q-1} j}) &= \gamma_j(\theta_{i_q j} - \theta_{i_{q-1} j}) - \gamma_j(\varepsilon_{i_q j} + \varepsilon_{i_{q-1} j}) \\ &= \ell - \frac{\ell}{2} = \frac{\ell}{2} \end{aligned}$$

and

$$\gamma_j(\theta_{i_{1j}} - \varepsilon_{i_{1j}}) - w_{n-1} = \ell - \frac{\ell}{4} = \frac{3\ell}{4}.$$

Therefore,  $(Z^\ell, \varepsilon^\ell) \sim_S (Z^0, 0)$  and  $(\theta^\ell, \varepsilon^\ell) \in Q^{j,n}(Z^0)$ . As  $\ell \rightarrow \infty$ ,  $\varepsilon_{i_{qj}}^\ell \rightarrow \infty$  so  $m_{i_{qj}}(\varepsilon_{i_{qj}}^\ell) \rightarrow 0$  for each  $q$ . ■

If all thresholds  $\theta_{ij}^0$  are greater than the largest value of  $\Lambda_j$ , then all slopes  $m_{ij}$  can be made arbitrarily small. Therefore,  $j$  does not play a role in the optimization. We state this formally after the following definition.

**Definition 6.3.** If  $\theta_{ij} > w_{n-1}$  for all  $i \in \mathbf{T}(j)$ , that is,  $B^{j,n}(\theta) = \mathbf{T}(j)$ , then we say  $j$  is *redundant*. Otherwise,  $j$  is *irredundant*.

**Proposition 5.** Let  $j$  be redundant. Then

$$\inf_{(\theta, \varepsilon) \in Q^{j,n}(Z^0)} \max_{i \in \mathbf{T}(j)} \{m_{ij}(\varepsilon_{ij})\} = 0.$$

*Proof.*  $B^{j,n}(\theta) = \mathbf{T}(j)$  so the result follows from Lemma 5. ■

**Corollary 6.1.** Suppose every node is redundant. Then

$$\max_{j=1, \dots, N} \inf_{(\theta, \varepsilon) \in \overline{Q}(Z^0)} \max_{i \in \mathbf{T}(j)} \{m_{ij}(\varepsilon_{ij})\} = 0.$$

If  $j$  is irredundant, we would still like to make an explicit choice of  $(\theta^{j,n}, \varepsilon^{j,n}) \in Q^{j,n}(Z^0)$  so that we can construct an optimal  $\theta^j$  explicitly. The following definition describes such a choice and the proposition that follows constructs  $\theta^j$  from the  $\theta^{j,n}$ .

**Definition 6.4.** When  $j$  is irredundant, we define

$$D^{j,n} = \min_{p < n} \{D^{j,p}\}.$$

Letting  $B^{j,n}(\theta^0) = \{i_1, \dots, i_k\}$  with  $\theta_{i_{1j}}^0 < \dots < \theta_{i_{kj}}^0$ , we define  $(\theta^{j,n}, \varepsilon^{j,n}) \in Q^{j,n}(Z^0)$  to be consistent with Definition 6.2 and Lemma 3. That is,

$$\begin{aligned} \theta_{i_{1j}}^{j,n} &= w_{n-1} + \Delta_{i_{1j}} D^{j,n} \\ \theta_{i_{qj}}^{j,n} &= \theta_{i_{q-1j}}^{j,n} + (\Delta_{i_{q-1j}} + \Delta_{i_{qj}}) D^{j,n}, \quad \text{if } q > 1, \text{ and} \\ \varepsilon_{i_{qj}}^{j,n} &= \Delta_{i_{qj}} D^{j,n}. \end{aligned}$$

**Proposition 6.** Let  $j \in V$  be irredundant. Define  $(\theta^j, \varepsilon^j) \in \overline{Q^j}(Z^0)$  by

$$\begin{aligned} \theta_{ij}^j &= \theta_{ij}^{j,p}, \quad i \in B^{j,p}(\theta^0) \\ \varepsilon^j &= \sum_{p=1}^n \varepsilon^{j,p}. \end{aligned}$$

Then (17) is achieved at  $(\theta^j, \varepsilon^j)$ .

*Proof.* For  $i_0 \notin B^{j,p}(\theta^0)$ , (18) is independent of  $\theta_{i_0j}$  and  $\varepsilon_{i_0j}$ . Therefore, by Lemma 4, for all  $p < n$

$$\min_{(\theta, \varepsilon) \in \overline{Q^{j,p}}(Z^0)} \max_{i \in B^{j,p}(\theta)} \{m_{ij}(\varepsilon_{ij})\}$$

is achieved at  $(\theta^j, \varepsilon^j)$ . From the definition of  $(\theta^{j,n}, \varepsilon^{j,n})$ ,

$$\max_{i \in B^{j,n}(\theta^{j,n})} \{m_{ij}(\varepsilon_{ij}^{j,n})\} = \max_{p < n} \max_{i \in B^{j,p}(\theta^j)} \{m_{ij}(\varepsilon_{ij}^j)\}.$$

Since  $\mathbf{T}(j) = \bigcup_{p=1}^n B^{j,p}(\theta^0)$ , (17) is then achieved at  $(\theta^j, \varepsilon^j)$ . ■

See Figure 4 for the optimal pair  $(\theta^j, \varepsilon^j)$  as defined in Proposition 6 where  $j$  is an irredundant node. Finally, we construct the optimal  $\theta$  from the  $\theta^j$ . First, we need to define  $\theta^j$  when  $j$  is redundant. As the slopes  $m_{ij}$  can be made arbitrarily small, by Proposition 5, we may choose  $(\theta^j, \varepsilon^j) \in \overline{Q^j(Z^0)}$  so that

$$\max_{i \in \mathbf{T}(j)} \{m_{ij}(\varepsilon_{ij}^j)\} < \max\{m_{ik}(\varepsilon_{ik}^k) \mid k \text{ is irredundant and } i \in \mathbf{T}(k)\}.$$

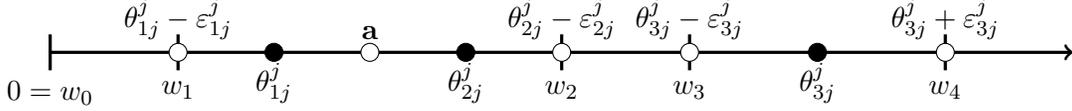


Fig. 4. **Optimal pair  $(\theta^j, \varepsilon^j)$  for a node  $j$  with two sources and three targets.** Since  $j$  has two sources,  $\Lambda_j$  takes 4 values and  $W_j = \{0 = w_0 < w_1 < w_2 < w_3 < w_4 < w_5 = \infty\}$ . The vertical lines indicate the values of  $w_0, \dots, w_4$ , which are identical to the values in Figure 3. We assume  $\gamma_j = 1$ ,  $\mathbf{T}(j) = \{1, 2, 3\}$  with  $\theta_{1j}^0 < \theta_{2j}^0 < \theta_{3j}^0$ , and  $\Delta_{1j} = \Delta_{2j}$ . The filled circles indicate the values of the thresholds. The unfilled circles indicate the values of  $\theta_{ij}^j \pm \varepsilon_{ij}^j$  where  $(\theta^j, \varepsilon^j) \in \overline{Q^j(Z^0)}$  is chosen as in Proposition 6. The pair  $(\theta^j, \varepsilon^j)$  is obtained from the optimal pairs  $(\theta^{j,2}, \varepsilon^{j,2}) \in \overline{Q^{j,2}(Z^0)}$  and  $(\theta^{j,4}, \varepsilon^{j,4}) \in \overline{Q^{j,4}(Z^0)}$ . The pair  $(\theta^{j,2}, \varepsilon^{j,2})$  is chosen so that the two disjoint open intervals  $(w_1, a)$  and  $(a, w_2)$  have equal length, where the endpoints are related to  $(\theta^{j,2}, \varepsilon^{j,2})$  by  $w_1 = \theta_{1j}^{j,2} - \varepsilon_{1j}^{j,2}$ ,  $a = \theta_{1j}^{j,2} + \varepsilon_{1j}^{j,2} = \theta_{2j}^{j,2} - \varepsilon_{2j}^{j,2}$ , and  $\theta_{2j}^{j,2} + \varepsilon_{2j}^{j,2} = w_2$ . The pair  $(\theta^{j,4}, \varepsilon^{j,4})$  is chosen so that  $(w_3, w_4) = (\theta_{3j}^{j,4} - \varepsilon_{3j}^{j,4}, \theta_{3j}^{j,4} + \varepsilon_{3j}^{j,4})$ .

**Theorem 10.** *Suppose there is an irredundant node. Define  $(\theta, \varepsilon) \in \overline{Q(Z^0)}$  by*

$$\theta_{ij} = \theta_{ij}^j \quad \text{and} \quad \varepsilon = \sum_{j=1}^N \varepsilon^j.$$

*Then the optimal solution of (16) is achieved at  $(\theta, \varepsilon)$ .*

*Proof.* For  $k \neq j$ , (17) is independent of  $\theta_{ik}$  and  $\varepsilon_{ik}$ . Therefore, by Proposition 6,  $(\theta, \varepsilon)$  achieves (17) for each irredundant  $j$ . For  $j$  redundant, we have chosen  $(\theta^j, \varepsilon^j)$  so that  $m_{ij}(\varepsilon_{ij}^j)$  is less than the maximum of the slopes over the irredundant nodes. Therefore, (16) is achieved at  $(\theta, \varepsilon)$ . ■

We finish by noting that degenerate bifurcations can occur at the optimal  $(\theta, \varepsilon)$  defined in Theorem 10. For example, the pitchfork-like bifurcation described in Proposition 3 occurs at such  $(\theta, \varepsilon)$  whenever  $\mathcal{R}(Z, \varepsilon)$  is a positive CFS and  $Z$  is chosen so that the loop characteristic cell  $\tau$  is an equilibrium cell. This was how the pair  $(\theta, \varepsilon)$  used to create Figure 2(d) was chosen.

## 7. Proof of Theorem 1

To prove Theorem 1, we extend the notion of *labeling map* and *flow direction map*, defined in [Duncan *et al.*, 2021] for switching systems, to ramp systems. For a regular switching parameter  $Z$  and loop characteristic cell  $\tau$ , the labeling map describes the crossing direction of trajectories across a given neighbor of  $\tau$  (see Figure 5). Regular parameters were defined precisely so that these crossing directions are well defined. The flow direction map then summarizes the labeling map across all neighbors of  $\tau$ . The extended maps have an identical role in ramp systems. The main insight is that the perturbed flow direction map defined for ramp systems agrees with the unperturbed flow direction map when  $Z$  and  $(Z, \varepsilon)$  are strongly equivalent (Theorem 11). Since Theorem 3.11 of [Duncan *et al.*, 2021] gives a characterization of SWITCH-equilibrium cells through the flow direction map, this allows us to prove the correspondence between equilibrium cells.

**Definition 7.1.** Let  $Z$  be a switching parameter and  $Z \sim_W (Z, \varepsilon)$ .

- (1) The *labeling map*  $\mathcal{L} : \text{LCC} \times V \times \{-, +\} \times \mathbf{R}_+^{N \times N} \rightarrow \{-1, 1\}$  describes the sign of the right hand side of the ramp system on the cells that are neighbors of  $\tau \in \text{LCC}$  in a particular direction. Letting  $\rho = \rho^\tau$ ,

we first consider regular directions  $j \notin \text{sd}(\tau)$ . Here we look at the sign of the  $j$ -th equation of the ramp system (4) on the boundary in the  $j$ -th direction

$$\mathcal{L}(\tau, j, \beta; \varepsilon) := \begin{cases} \text{sgn}(-\gamma_j(\theta_{a_j^+} + \varepsilon_{a_j^+}) + \Lambda_j(\tau)), & j \notin \text{sd}(\tau), \beta = - \\ \text{sgn}(-\gamma_j(\theta_{b_j^+} - \varepsilon_{b_j^+}) + \Lambda_j(\tau)), & j \notin \text{sd}(\tau), \beta = + \end{cases}$$

For singular direction  $j \in \text{sd}(\tau)$ , we look at a  $j$ -neighbor of  $\tau$  and ask for the sign of the  $\rho(j)$ -th equation of the ramp system because  $\Lambda_{\rho(j)}$  is guaranteed to be well defined on a  $j$ -neighbor (see Lemma 2):

$$\mathcal{L}(\tau, j, \beta; \varepsilon) := \begin{cases} \text{sgn}(-\gamma_{\rho(j)}(\theta_{\rho^2(j)\rho(j)} - \beta\varepsilon_{\rho^2(j)\rho(j)}) + \Lambda_{\rho(j)}(\tau_j^-)), & j \in \text{sd}(\tau), \beta = - \\ \text{sgn}(-\gamma_{\rho(j)}(\theta_{\rho^2(j)\rho(j)} + \beta\varepsilon_{\rho^2(j)\rho(j)}) + \Lambda_{\rho(j)}(\tau_j^+)), & j \in \text{sd}(\tau), \beta = +. \end{cases}$$

(2) The *flow direction map*,  $\Phi(\cdot; \varepsilon) : \text{LCC} \times \mathbf{R}_+^{N \times N} \rightarrow \{-1, 0, 1\}^N$  summarizes the degree of agreement in the labeling map between the neighbors of  $\tau$  in a given direction. It is defined component-wise by

$$\Phi_j(\tau; \varepsilon) := \begin{cases} 1, & \mathcal{L}(\tau, j, -; \varepsilon) = 1 = \mathcal{L}(\tau, j, +; \varepsilon) \\ -1, & \mathcal{L}(\tau, j, -; \varepsilon) = -1 = \mathcal{L}(\tau, j, +; \varepsilon) \\ 0, & \mathcal{L}(\tau, j, -; \varepsilon) = -\mathcal{L}(\tau, j, +; \varepsilon). \end{cases}$$

**Theorem 11.** *Let  $Z \sim_S (Z, \varepsilon)$ . Then for each  $\tau \in \text{LCC}$ ,  $j \in V$ , and  $\beta \in \{-, +\}$ ,*

$$\mathcal{L}(\tau, j, \beta; 0) = \mathcal{L}(\tau, j, \beta; \varepsilon).$$

Consequently,  $\Phi(\tau; \varepsilon) = \Phi(\tau; 0)$ .

*Proof.* First suppose  $j$  is a regular direction of  $\tau$ . Let  $A \in \text{In}_j$  be the input combination such that the  $\Lambda$ -valuation function evaluated at  $A$  satisfies  $\omega_j(A) = \Lambda_j(\tau)$ . Strong equivalence implies the following list of equivalent statements

$$\begin{aligned} \mathbb{L}_j(A, a_j^+, +; \varepsilon) &= \mathbb{L}_j(A, a_j^+, +; 0), \\ \text{sgn}(-\gamma_j(\theta_{a_j^+} + \varepsilon_{a_j^+}) + \Lambda_j(\tau)) &= \text{sgn}(-\gamma_j\theta_{a_j^+} + \Lambda_j(\tau)), \\ \mathcal{L}(\tau, j, -; \varepsilon) &= \mathcal{L}(\tau, j, -; 0). \end{aligned}$$

A similar computation shows  $\mathcal{L}(\tau, j, +; \varepsilon) = \mathcal{L}(\tau, j, +; 0)$ .

Now suppose  $j \in \text{sd}(\tau)$ . Let  $\rho = \rho^\tau$  and  $A \in \text{In}_{\rho(j)}$  such that  $\omega_{\rho(j)}(A) = \Lambda_{\rho(j)}(\tau_j^+)$ . Strong equivalence implies

$$\begin{aligned} \mathbb{L}_{\rho(j)}(A, \rho^2(j), +; \varepsilon) &= \mathbb{L}_{\rho(j)}(A, \rho^2(j), +; 0), \\ \text{sgn}(-\gamma_{\rho(j)}(\theta_{\rho^2(j)\rho(j)} + \varepsilon_{\rho^2(j)\rho(j)}) + \Lambda_{\rho(j)}(\tau_j^+)) &= \text{sgn}(-\gamma_{\rho(j)}\theta_{\rho^2(j)\rho(j)} + \Lambda_{\rho(j)}(\tau_j^+)), \\ \mathcal{L}(\tau, j, +; \varepsilon) &= \mathcal{L}(\tau, j, +; 0). \end{aligned}$$

A similar computation shows  $\mathcal{L}(\tau, j, -; \varepsilon) = \mathcal{L}(\tau, j, -; 0)$ . ■

## 7.1. Technical Lemmas

To prove Theorem 1, we will need some technical lemmas. The following lemma implies statements 3 and 6 of Lemma 1.

**Lemma 6.** *Let  $(Z, \varepsilon) \sim_W Z$  and  $\tau \in \chi(0)$ . If  $\sigma_{ij}(\tau)$  is well defined, then  $R_{ij}(x; \varepsilon) = \sigma_{ij}(\tau)$  for all  $x \in \tau(\varepsilon)$ . Consequently, if  $\Lambda_i(\tau)$  is well defined then  $R_i(x, \varepsilon) = \Lambda_i(\tau)$  for all  $x \in \tau(\varepsilon)$ .*

*Proof.* Let  $\rho = \rho^\tau$  and suppose  $\sigma_{ij}(\tau)$  is well defined. First suppose  $j \in \text{sd}(\tau)$  with  $\pi_j(\tau) = \{\theta_{i_0j}\}$ . Since  $\sigma_{ij}(\tau)$  is well defined,  $i_0 \neq i$ . We have  $\pi_j(\tau(\varepsilon)) = (\theta_{i_0j} - \varepsilon_{i_0j}, \theta_{i_0j} + \varepsilon_{i_0j})$  and weak equivalence implies that for  $x \in \tau(\varepsilon)$ ,  $x_j < \theta_{i_0j} - \varepsilon_{i_0j}$  if  $\theta_{ij} < \theta_{i_0j}$  and  $x_j > \theta_{i_0j} + \varepsilon_{i_0j}$  if  $\theta_{ij} > \theta_{i_0j}$ . Therefore  $R_{ij}(x; \varepsilon) = \sigma_{ij}(\tau)$ .

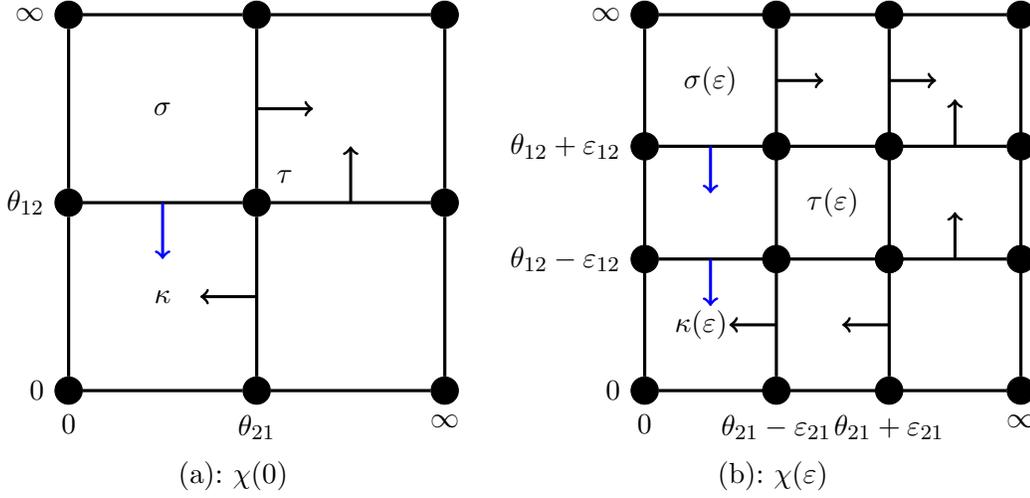


Fig. 5. **The labeling map  $\mathcal{L}$  represented as arrows on the cell complex.** Cell complexes and the labeling map for the positive toggle switch network at a parameter  $Z$  satisfying  $L_{12} < \theta_{21} < U_{12}$ ,  $L_{12} < \theta_{21} < U_{12}$  and  $(Z, \varepsilon) \sim_S Z$ . We do not draw the arrows on the boundary of phase space, which point inwards for any choice of parameters. **(a):** The blue arrow represents  $\mathcal{L}(\kappa, 2, +; 0)$  and  $\mathcal{L}(\sigma, 2, -; 0)$  for which 2 is a regular direction. This arrow also represents  $\mathcal{L}(\tau, 1, -; 0)$  for LCC  $\tau$  for which  $1 \in \text{sd}(\tau)$ . All these values are equal to  $-1$  so the arrow points down. Since the arrows on the outer boundary of the complex point inwards,  $\Phi_2(\kappa; 0) = 0$  and  $\Phi_2(\sigma; 0) = -1$ . Since the arrow originating from  $\tau_1^+$  points up, and  $\mathcal{L}(\tau, 1, -; 0) = -1$ , we have  $\Phi_1(\tau; 0) = 0$ . **(b):** The top blue arrow represents  $\mathcal{L}(\sigma, 2, -; \varepsilon)$ , while the bottom blue arrow represents  $\mathcal{L}(\kappa, 2, +; \varepsilon)$  and  $\mathcal{L}(\tau, 1, -; \varepsilon)$ . These arrows point down by Theorem 11.

If  $j \notin \text{sd}(\tau)$ , then  $\pi_j(\tau) = (\theta_{a_j j} + \varepsilon_{a_j j}, \theta_{b_j j} - \varepsilon_{b_j j})$ . Weak equivalence implies that for  $x \in \tau(\varepsilon)$ ,  $x_j < \theta_{ij} - \varepsilon_{ij}$  if  $\theta_{ij} < \theta_{a_j j}$  and  $x_j > \theta_{ij} + \varepsilon_{ij}$  if  $\theta_{ij} > \theta_{b_j j}$ . Therefore  $R_{ij}(x; \varepsilon) = \sigma_{ij}(\tau)$ .

The function  $\Lambda_i(\tau) = \prod \sum \sigma_{ij}(\tau)$  is well defined if and only if  $\sigma_{ij}(\tau)$  is well defined for all  $j \in \mathbf{S}(i)$ . Since  $\sigma_{ij}(\tau) = R_{ij}(x; \varepsilon)$  for all  $x \in \tau(\varepsilon)$ , we have  $\Lambda_i(\tau) = \prod \sum R_{ij}(x; \varepsilon) = R_i(x; \varepsilon)$ .  $\blacksquare$

Next, we provide a relationship between the process of going from a cell  $\tau \in \chi(0)$  to the corresponding cell  $\tau(\varepsilon) \in \chi(\varepsilon)$  and the process of taking a neighbor.

**Lemma 7.** *Let  $Z \sim_W (Z, \varepsilon)$ ,  $\tau \in \chi(0)$  and  $s \in \text{sd}(\tau)$ . If  $\pi_s(\tau) \neq \{\theta_{\infty s}\}$  then  $\tau(\varepsilon)_s^+$  is the left  $s$ -neighbor of  $\tau_s^+(\varepsilon)$ . If  $\pi_s(\tau) \neq \{\theta_{-\infty s}\}$  then  $\tau(\varepsilon)_s^-$  is the right  $s$ -neighbor of  $\tau_s^-(\varepsilon)$ . In general, for  $\beta \in \{-, +\}$  and  $\tau \subset \mathbf{R}_+^N$ ,  $\tau(\varepsilon)_s^\beta$  is an  $s$ -neighbor of  $\tau_s^\beta(\varepsilon)$ .*

*Proof.* For  $i \neq s$  we have  $\pi_i(\tau_s^\beta) = \pi_i(\tau)$  so

$$\pi_i(\tau_s^\beta(\varepsilon)) = \pi_i(\tau(\varepsilon)) = \pi_i(\tau(\varepsilon)_s^\beta).$$

Let  $\rho = \rho^\tau$ . Since  $\pi_s(\tau_s) \neq \{\theta_{\infty s}\}$ , we have

$$\begin{aligned} \pi_s(\tau_s^+) &= (\theta_{\rho(s)s}, \theta_{\rho_+(s)s}) \\ \pi_s(\tau_s^+(\varepsilon)) &= (\theta_{\rho(s)s} + \varepsilon_{\rho(s)s}, \theta_{\rho_+(s)s} - \varepsilon_{\rho_+(s)s}) \end{aligned}$$

and

$$\begin{aligned} \pi_s(\tau(\varepsilon)) &= (\theta_{\rho(s)s} - \varepsilon_{\rho(s)s}, \theta_{\rho(s)s} + \varepsilon_{\rho(s)s}) \\ \pi_s(\tau(\varepsilon)_s^+) &= \{\theta_{\rho(s)s} + \varepsilon_{\rho(s)s}\}. \end{aligned}$$

Notice that  $\pi_s(\tau(\varepsilon)_s^+)$  is the left end point of  $\pi_s(\tau_s^+(\varepsilon))$ . All other projections agree. Therefore,  $\tau(\varepsilon)_s^+$  is the left  $s$ -neighbor of  $\tau_s^+(\varepsilon)$ . A similar argument shows that  $\tau(\varepsilon)_s^-$  is the right  $s$ -neighbor of  $\tau_s^-(\varepsilon)$ .  $\blacksquare$

Finally, we prove that there are no singular  $\mathcal{R}$ -equilibrium cells if  $Z$  and  $(Z, \varepsilon)$  are strongly equivalent.

**Lemma 8.** *If  $Z \sim_S (Z, \varepsilon)$  and  $\sigma \in \chi(\varepsilon)$  is a singular cell, then  $\sigma$  does not contain an equilibrium of  $\mathcal{R}(Z, \varepsilon)$ .*

*Proof.* For the sake of contradiction, suppose  $\sigma \in \chi(\varepsilon)$  is a singular cell containing an equilibrium of  $\mathcal{R}(Z, \varepsilon)$ . Let  $x$  be that equilibrium. For each singular direction  $s$  of  $\sigma$ , we write  $\pi_s(\sigma) = \{\theta_{i_s s} + \beta_s \varepsilon_{i_s s}\}$  for  $\beta_s \in \{-1, 1\}$ . For each regular direction  $r$  of  $\sigma$  we write

$$\pi_r(\sigma) = (\theta_{i_r r} - \varepsilon_{i_r r}, \theta_{i_r r} + \varepsilon_{i_r r}) \quad \text{or} \quad \pi_r(\sigma) = (\theta_{i_r^1 r} + \varepsilon_{i_r^1 r}, \theta_{i_r^2 r} - \varepsilon_{i_r^2 r}).$$

We define a cell  $\tau \in \chi(0)$  by its projections. For each singular direction  $s$  of  $\sigma$ , we let  $\theta_{i_s^1 s} < \theta_{i_s s} < \theta_{i_s^2 s}$  be consecutive thresholds and define

$$\pi_s(\tau) := \begin{cases} (\theta_{i_s^1 s}, \theta_{i_s s}), & \beta_s = -1 \\ (\theta_{i_s s}, \theta_{i_s^2 s}), & \beta_s = 1 \end{cases}$$

and for each regular direction  $r$  we define

$$\pi_r(\tau) := \begin{cases} \{\theta_{i_r r}\}, & \pi_r(\sigma) = (\theta_{i_r r} - \varepsilon_{i_r r}, \theta_{i_r r} + \varepsilon_{i_r r}) \\ (\theta_{i_r^1 r}, \theta_{i_r^2 r}), & \pi_r(\sigma) = (\theta_{i_r^1 r} + \varepsilon_{i_r^1 r}, \theta_{i_r^2 r} - \varepsilon_{i_r^2 r}). \end{cases}$$

We note that  $\sigma \subset \overline{\tau(\varepsilon)}$ .

If  $\tau$  is a loop characteristic cell, then for a singular direction  $s$  of  $\sigma$ ,  $s$  is regular direction of  $\tau$ . Therefore  $\Lambda_s(\tau)$  is well defined and by Lemma 1 and continuity of  $R$ ,  $R_s(x; \varepsilon) = \Lambda_s(\tau)$ . Since  $x$  is an equilibrium, we have  $-\gamma_s(\theta_{i_s s} + \beta_s \varepsilon_{i_s s}) + \Lambda_s(\tau) = 0$ , contradicting that  $(Z, \varepsilon)$  is regular.

If  $\tau$  is not a loop characteristic cell, then there is a singular direction  $j$  of  $\tau$  so that  $j \notin \rho^\tau(\text{sd}(\tau))$ . By Lemma 1,  $\Lambda_j(\tau) = R_j(x; \varepsilon)$ . Since  $x$  is an equilibrium,  $-\gamma_j x_j + \Lambda_j(\tau) = 0$ . As  $x_j \in (\theta_{i_j j} - \varepsilon_{i_j j}, \theta_{i_j j} + \varepsilon_{i_j j})$ , we have

$$-\gamma_j(\theta_{i_j j} - \varepsilon_{i_j j}) + \Lambda_j(\tau) = 1 \quad \text{and} \quad -\gamma_j(\theta_{i_j j} + \varepsilon_{i_j j}) + \Lambda_j(\tau) = -1.$$

So, there is an  $A \in \text{In}_j$  so that  $L_j(A, i_j, -, \varepsilon) = 1$  and  $L_j(A, i_j, -, \varepsilon) = -1$ . Strong equivalence implies this holds for all  $\varepsilon$  so that  $-\gamma_j \theta_{i_j j} + \Lambda_j(\tau) = 0$ , contradicting that  $(Z, \varepsilon)$  is regular. ■

## 7.2. Proof of Theorem 1

Let  $\tau \in \chi(0)$  be an equilibrium cell. By Theorem 3.11 of [Duncan *et al.*, 2021],  $\tau$  is a loop characteristic cell so that by Lemma 1,  $\Lambda_r(\tau)$  is well defined for each regular direction  $r$  and  $\Lambda_{\rho(s)}(\tau_s^\pm)$  is well defined for each singular direction  $s$ . Additionally, by Theorem 11,  $\Phi(\tau; \varepsilon) = \Phi(\tau; 0)$ .

Let  $r$  be a regular direction of  $\tau$ . By Lemma 6 the dynamics of  $\mathcal{R}(Z, \varepsilon)$  satisfy

$$\dot{x}_r = -\gamma_r x_r + R_r(x; \varepsilon) = -\gamma_r x_r + \Lambda_r(\tau) \tag{19}$$

on  $\tau(\varepsilon)$ .  $\Phi_r(\tau; \varepsilon) = \Phi_r(\tau; 0) = 0$  so  $\pi_r(\tau(\varepsilon))$  is an invariant set for (19). Since (19) is linear on  $\pi_r(\tau(\varepsilon))$  there is a unique stable equilibrium in  $\pi_r(\tau(\varepsilon))$ . This shows that if  $\tau$  is a regular equilibrium cell,  $\tau(\varepsilon)$  contains a unique stable equilibrium.

Let  $s \in \text{sd}(\tau)$  and  $\rho = \rho^\tau$ . On  $\tau(\varepsilon)$ ,  $R_{\rho(s)}(x; \varepsilon)$  depends only on the value of  $x_s$ . Since  $\Phi_{\rho(s)}(\tau, \varepsilon) = 0$ , for each  $x \in \tau(\varepsilon)$

$$\begin{aligned} \text{sgn}(-\gamma_{\rho(s)}(\theta_{\rho^2(s)\rho(s)} - \varepsilon_{\rho^2(s)\rho(s)}) + R_{\rho(s)}(x; \varepsilon)) \\ = -\text{sgn}(-\gamma_{\rho(s)}(\theta_{\rho^2(s)\rho(s)} + \varepsilon_{\rho^2(s)\rho(s)}) + R_{\rho(s)}(x; \varepsilon)). \end{aligned}$$

By the intermediate value theorem and monotonicity of  $-\gamma_{\rho(s)} x_{\rho(s)} + R_{\rho(s)}(x; \varepsilon)$  in  $x_{\rho(s)}$ , for every value of  $x_s$  there is a unique value of  $x_{\rho(s)}$ ,  $x_{\rho(s)}^*(x_s)$ , so that

$$-\gamma_{\rho(s)} x_{\rho(s)}^*(x_s) + R_{\rho(s)}(x; \varepsilon) = 0.$$

By continuity of  $R_{\rho(s)}$ ,  $x_{\rho(s)}^*(\cdot)$  can be defined on  $\overline{\pi_s(\tau(\varepsilon))}$ . Define

$$g : \prod_{s \in \text{sd}(\tau)} \overline{\pi_s(\tau)} \rightarrow \prod_{s \in \text{sd}(\tau)} \overline{\pi_s(\tau)}, \quad g := (g_1, \dots, g_N)$$

by  $g_s(x) := x_s^*(x_{\rho^{-1}(s)})$ . Brouwer's fixed point theorem implies there is a fixed point of  $g$  so that  $-\gamma_{\rho(s)}x_{\rho(s)} + \mathbf{R}(x; \varepsilon)$  can be solved simultaneously for each  $s \in \text{sd}(\tau)$ . This shows existence of an equilibrium of  $\mathcal{R}(Z, \varepsilon)$  in  $\tau(\varepsilon)$  and proves the backward direction of the Theorem. We now prove the forward direction.

Let  $\sigma \in \chi(\varepsilon)$  be a cell which contains an equilibrium of  $\mathcal{R}(Z, \varepsilon)$ . Lemma 8 implies that  $\sigma$  is a regular cell. Since there is a bijection between regular cells of the ramp complex  $\chi(\varepsilon)^{(N)}$  and all cells of the switching complex  $\chi(0)$ , we may write  $\sigma = \tau(\varepsilon)$  for  $\tau \in \chi(0)$ .

Suppose  $\tau$  is not a loop characteristic cell. Then there is an  $s \in \text{sd}(\tau)$  so that  $s \notin \rho(\text{sd}(\tau))$ . By Lemma 1,  $\Lambda_s(\tau) = \mathbf{R}_s(x; \varepsilon)$  for each  $x \in \tau(\varepsilon)$ . Since the cell  $\tau(\varepsilon)$  contains an equilibrium, there is an  $x \in \tau(\varepsilon)$  so that

$$0 = -\gamma_s x_s + \mathbf{R}_s(x; \varepsilon) = -\gamma_s x_s + \Lambda_s(\tau).$$

Since  $s$  is a singular direction,  $\pi_s(\tau) = \{\theta_{\rho(s)s}\}$ . Therefore  $x_s \in \pi_s(\tau(\varepsilon)) = (\theta_{\rho(s)s} - \varepsilon_{\rho(s)s}, \theta_{\rho(s)s} + \varepsilon_{\rho(s)s})$  which implies

$$\begin{aligned} \text{sgn}(-\gamma_s(\theta_{\rho(s)s} - \varepsilon_{\rho(s)s}) + \Lambda_s(\tau)) &= 1 \\ \text{sgn}(-\gamma_s(\theta_{\rho(s)s} + \varepsilon_{\rho(s)s}) + \Lambda_s(\tau)) &= -1. \end{aligned}$$

Therefore, there is an  $A \in \text{In}_s$  such that

$$\mathbf{L}_s(A, \rho(s), +; \varepsilon) = -\mathbf{L}_s(A, \rho(s), -; \varepsilon).$$

Strong equivalence implies that for every  $\varepsilon' \leq \varepsilon$  and  $\beta \in \{-, +\}$ ,  $\mathbf{L}_s(A, \rho(s), \beta; \varepsilon) = \mathbf{L}_s(A, \rho(s), \beta; \varepsilon')$ . This can only hold if  $-\gamma_s \theta_{\rho(s)s} + \Lambda_s(\tau) = 0$ . This contradicts the assumption that  $Z$  is a regular parameter. This contradiction shows that  $\tau$  must be a loop characteristic cell. By Proposition 11, this implies  $\Phi(\tau; \varepsilon) = \Phi(\tau; 0)$ .

Now we will show that  $\Phi_j(\tau; \varepsilon) = 0$  for each  $j$ . We consider regular and singular directions separately.

Let  $r$  be a regular direction of  $\tau$ . Then for every  $x \in \tau(\varepsilon)$ ,  $\mathbf{R}_r(x; \varepsilon) = \Lambda_r(\tau)$ . Since the cell  $\tau(\varepsilon)$  contains an equilibrium, there is an  $x \in \tau(\varepsilon)$  so that

$$0 = -\gamma_r x_r + \mathbf{R}_r(x; \varepsilon) = -\gamma_r x_r + \Lambda_r(\tau).$$

Since  $x_r \in (\theta_{a_r r} + \varepsilon_{a_r r}, \theta_{b_r r} - \varepsilon_{b_r r})$ ,

$$\begin{aligned} \text{sgn}(-\gamma_r(\theta_{a_r r} + \varepsilon_{a_r r}) + \Lambda_r(\tau)) &= 1 \\ \text{sgn}(-\gamma_r(\theta_{b_r r} - \varepsilon_{b_r r}) + \Lambda_r(\tau)) &= -1 \end{aligned}$$

or, equivalently,  $\mathcal{L}(\tau, r, -; \varepsilon) = -\mathcal{L}(\tau, r, +; \varepsilon)$  so that  $\Phi_r(\tau; \varepsilon) = 0$ .

Let  $s$  be a singular direction of  $\tau$ . Assume, by a way of contradiction, that  $\Phi_s(\tau; \varepsilon) \neq 0$ . This means that either  $\mathcal{L}(\tau, s, \pm; \varepsilon) = 1$  or  $\mathcal{L}(\tau, s, \pm; \varepsilon) = -1$ . Assume without loss that  $\mathcal{L}(\tau, s, \pm; \varepsilon) = 1$ . Then

$$\text{sgn}(-\gamma_{\rho(s)}(\theta_{\rho^2(s)\rho(s)} \pm \varepsilon_{\rho^2(s)\rho(s)}) + \Lambda_{\rho(s)}(\tau_s^\pm)) = 1.$$

By Lemma 1, for every  $x \in \tau_s^\pm(\varepsilon)$ ,  $\mathbf{R}_{\rho(s)}(x; \varepsilon) = \Lambda_{\rho(s)}(\tau_s^\pm)$ . By Lemma 7,  $\tau(\varepsilon)_s^\pm \in \chi^{(N-1)}(\varepsilon)$  is a neighbor of  $\tau_s^\pm(\varepsilon)$ . By continuity of  $\mathbf{R}$ , for every  $x \in \tau(\varepsilon)_s^\pm$ ,  $\mathbf{R}_{\rho(s)}(x; \varepsilon) = \Lambda_{\rho(s)}(\tau_s^\pm)$ . Therefore we conclude that for  $x \in \tau(\varepsilon)_s^-$  or  $x \in \tau(\varepsilon)_s^+$ , we have

$$\text{sgn}(-\gamma_{\rho(s)}(\theta_{\rho^2(s)\rho(s)} \pm \varepsilon_{\rho^2(s)\rho(s)}) + \mathbf{R}_{\rho(s)}(x; \varepsilon)) = 1.$$

Since  $\mathbf{R}_{\rho(s)}$  is monotone in  $x_s$  and depends only on  $x_s$  on  $\tau(\varepsilon)$ , the previous equation holds for all  $x \in \tau(\varepsilon)$ . On  $\tau(\varepsilon)$ ,  $x_{\rho(s)} \in (\theta_{\rho^2(s)\rho(s)} - \varepsilon_{\rho^2(s)\rho(s)}, \theta_{\rho^2(s)\rho(s)} + \varepsilon_{\rho^2(s)\rho(s)})$ , so for all  $x \in \tau(\varepsilon)$

$$\text{sgn}(-\gamma_{\rho(s)}x_{\rho(s)} + \mathbf{R}_{\rho(s)}(x; \varepsilon)) = 1.$$

But  $\tau(\varepsilon)$  contains an equilibrium so there is an  $x \in \tau(\varepsilon)$  so that  $-\gamma_{\rho(s)}x_{\rho(s)} + \mathbf{R}_{\rho(s)}(x; \varepsilon) = 0$ , a contradiction. A similar argument shows that the assumption  $\mathcal{L}(\tau, s, \pm; \varepsilon) = -1$  also leads to a contradiction. Therefore,  $\Phi_s(\tau; \varepsilon) = 0$ . We have shown  $\Phi_j(\tau; 0) = 0$  for all singular and all regular directions, and thus for all  $j$ . By Theorem 3.11 of [Duncan *et al.*, 2021],  $\tau$  is an equilibrium cell which proves the forward direction.

We now show that the equilibrium in  $\tau(\varepsilon)$  is unique. If not, then linearity of (4) on  $\tau(\varepsilon)$  implies that there is a line segment of equilibria in  $\tau(\varepsilon)$ , which extends to the boundary of  $\tau(\varepsilon)$ . In particular, there is a singular cell of the ramp complex containing an equilibrium, contradicting Lemma 8.

## 8. Proof of Bifurcation Results for CFS

Here we prove the results stated in Section 4.2. We divide this section into two parts. The first part addresses the degenerate bifurcations in positive CFN, and the second part addresses non-degenerate border crossing bifurcations.

### 8.1. Proof of Propositions 2 and 3

Before proving the propositions we set aside an argument used in both proofs as a lemma.

**Lemma 9.** *Let  $\mathbf{RN}$  be a positive CFN and  $Z$  be a switching parameter such that the singular loop characteristic cell  $\tau$  is an equilibrium cell. If  $Z \sim_S (Z, \varepsilon)$  then  $\mathcal{R}(Z, \varepsilon)$  has three equilibrium cells,  $\tau(\varepsilon)$ ,  $\kappa^L(\varepsilon)$ ,  $\kappa^H(\varepsilon)$  where*

$$\kappa^L := \prod_{j=1}^N (0, \theta_{(j+1)j}), \quad \text{and} \quad \kappa^H := \prod_{j=1}^N (\theta_{(j+1)j}, \infty).$$

Moreover, the equilibria in  $\kappa^L$  and  $\kappa^H$  are stable and the equilibrium in  $\tau$  is unstable.

*Proof.* By Lemma 4.4 of [Duncan *et al.*, 2021],  $\tau$ ,  $\kappa^L$ , and  $\kappa^H$  are SWITCH-equilibrium cells. Theorem 1 implies  $\tau(\varepsilon)$ ,  $\kappa^L(\varepsilon)$ , and  $\kappa^H(\varepsilon)$  are  $\mathcal{R}$ -equilibrium cells and that the equilibria in  $\kappa^L(\varepsilon)$  and  $\kappa^H(\varepsilon)$  are stable. Proposition 1 implies the equilibrium in  $\tau(\varepsilon)$  is unstable. ■

*Proof.* [Proof of Proposition 2] First suppose  $\varepsilon < \varepsilon^0$ . Note that  $Z \sim_S (Z, \varepsilon)$ . Then by Lemma 9,  $\mathcal{R}(Z, \varepsilon)$  has two stable equilibria and one unstable equilibrium.

Now we consider  $\varepsilon > \varepsilon^0$ . Assume that (1) holds. The proof for case (2) is similar. Let  $\kappa^H$  be defined as in Lemma 9. Choose  $\varepsilon > \varepsilon^0$  so that  $\gamma_j \theta_{(j+1)j} + \varepsilon_{(j+1)j} < U_{j-1}$  for each  $j$ . Then  $\Phi_j(\kappa^H; \varepsilon) = 0$  for each  $j$  so that  $\kappa^H(\varepsilon)$  is attracting and therefore contains a stable equilibrium. This equilibrium is unique in  $\kappa^H(\varepsilon)$  since  $R(x; \varepsilon)$  is constant on  $\kappa^H(\varepsilon)$  by Lemma 1.

Now we show that  $\kappa^H(\varepsilon)$  is the unique equilibrium cell. For the sake of contradiction, suppose there is an equilibrium  $x$  not contained in  $\kappa^H$ . Then  $x_j \leq \theta_{(j+1)j} + \varepsilon_{(j+1)j}$  for some  $j$ . Since  $x_j$  is an equilibrium,

$$-\gamma_j x_j + R_{j(j-1)}(x_{j-1}; \varepsilon) = 0$$

and  $x_j \leq \gamma_j(\theta_{(j+1)j} + \varepsilon_{(j+1)j}) < U_{j(j-1)}$  implies  $x_{j-1} < \theta_{j(j-1)} + \varepsilon_{j(j-1)}$ . An induction argument then implies  $x_j < \theta_{(j+1)j} + \varepsilon_{(j+1)j}$  for all  $j$ . Since  $R_{j(j-1)} \geq L_{j(j-1)}$  for all  $j$  and  $\gamma_j(\theta_{(j+1)j} - \varepsilon_{(j+1)j}) < L_{j(j-1)}$ , we must have  $x_j > \theta_{(j+1)j} - \varepsilon_{(j+1)j}$  for each  $j$ . Therefore we must have  $x_j \in (\theta_{(j+1)j} - \varepsilon_{(j+1)j}, \theta_{(j+1)j} + \varepsilon_{(j+1)j})$  for each  $j$ , i.e.  $x \in \tau(\varepsilon)$ .

We may choose  $\varepsilon > \varepsilon^0$  so that  $M(\varepsilon) > \prod_j \gamma_j$ . To see this, we compute

$$\begin{aligned} M(\varepsilon^0) &= \prod_j \frac{U_{(j+1)j} - L_{(j+1)j}}{2\varepsilon_{(j+1)j}^0} \\ &= \prod_j \frac{U_{(j+1)j} - \gamma_j(\theta_{j(j-1)} - \varepsilon_{j(j-1)}^0)}{2\varepsilon_{(j+1)j}^0} \\ &> \prod_j \frac{\gamma_j(\theta_{j(j-1)} + \varepsilon_{j(j-1)}^0) - \gamma_j(\theta_{j(j-1)} - \varepsilon_{j(j-1)}^0)}{2\varepsilon_{(j+1)j}^0} \\ &= \prod_j \frac{2\gamma_j \varepsilon_{j(j-1)}^0}{2\varepsilon_{(j+1)j}^0} = \prod_j \gamma_j. \end{aligned}$$

Since  $\det(J(x, \varepsilon)) = \prod_j \gamma_j - M(\varepsilon) \neq 0$ , we have  $x$  is the unique equilibrium in  $\tau(\varepsilon)$ . Therefore  $x$  and the equilibrium in  $\kappa^H$  are the unique equilibria of  $\mathcal{R}(Z, \varepsilon)$ .

To arrive at a contradiction we will use the Lefschetz-Hopf theorem

$$\sum_{x \in \text{Fix}(G)} i(G, x) = L_G,$$

applied to the map  $G : \mathbf{R}^N \rightarrow \mathbf{R}^N$  defined component-wise by

$$G_j(x) := -\gamma_j x_j + R_{j(j-1)}(x_{j-1}; \varepsilon).$$

In the Lefschetz-Hopf formula  $i(G, x)$  is the local index of the equilibrium  $x$  as a zero of a continuous function of  $G$ , and  $L_G$  is the Lefschetz number. Since the ramp system  $\mathcal{R}$  is dissipative, the function  $G(x)$  maps sufficiently large set  $[-K, K]^N$  to itself. At the same time, the equilibrium  $x^H$  in  $\kappa^H$  is locally stable and thus the index  $i(x^H, G) = L_G$ . Finally, since  $\det(J(x, \varepsilon)) \neq 0$ , the index  $i(x, G) \neq 0$ . This leads to a contradiction with the Lefschetz-Hopf formula. ■

*Proof.* [Proof of Proposition 3] First suppose  $\varepsilon < \varepsilon^0$ . Note that  $Z \sim_S (Z, \varepsilon)$ . By Lemma 9,  $\mathcal{R}(Z, \varepsilon)$  has two stable equilibria and one unstable equilibrium.

Now we consider  $\varepsilon > \varepsilon^0$ . Observe that  $U_{j(j-1)} + L_{j(j-1)} = 2\gamma_j(\theta_{(j+1)j})$  and  $U_{j(j-1)} - L_{j(j-1)} = 2\gamma_j \varepsilon_{(j+1)j}^0$  so that

$$\gamma_j \theta_{(j+1)j} = \frac{U_{j(j-1)} + L_{j(j-1)}}{2}, \quad \text{and} \quad \gamma_j \varepsilon_{(j+1)j}^0 = \Delta_{j(j-1)}/2$$

where  $\Delta_{(j+1)j} = U_{j(j-1)} - L_{j(j-1)}$ . For any  $\varepsilon > 0$ ,  $x \in \tau(\varepsilon)$  we have

$$-\gamma_j x_j + R_j(x; \varepsilon) = -\gamma_j x_j + \frac{U_{j(j-1)} + L_{j(j-1)}}{2} + \mathbf{s}_{j(j-1)} m_{j(j-1)}(x_{j-1} - \theta_{j(j-1)})$$

so that  $x^* := (\theta_{21}, \theta_{32}, \dots, \theta_{1N})$  is an equilibrium. To see that the equilibrium is stable for  $\varepsilon > \varepsilon^0$ , note that

$$m_{(j+1)j}(\varepsilon_{(j+1)j}^0) = \frac{\Delta_{(j+1)j}}{2\varepsilon_{(j+1)j}^0} = \gamma_j.$$

Since the slopes are decreasing in  $\varepsilon$ ,

$$R'_{(j+1)j}(x^*; \varepsilon) = m_{(j+1)j}(\varepsilon_{(j+1)j}) < \gamma_j.$$

Therefore the Jacobian evaluated at the equilibrium,  $J(x^*; \varepsilon)$  is strictly diagonally dominant and all eigenvalues have negative real part.

To see that  $x^*$  is the unique equilibrium, we first note that  $\mathcal{R}(Z, \varepsilon)$  is linear on  $\tau(\varepsilon)$  so that  $x$  is unique in  $\tau(\varepsilon)$ . Consider  $x^0 \notin \tau(\varepsilon)$ . Then there is an  $j$  so that  $x_{j-1}^0 \in [0, \theta_{j(j-1)} - \varepsilon_{j(j-1)}] \cup [\theta_{j(j-1)} + \varepsilon_{j(j-1)}, \infty)$ . By Lemma 1,  $R_j(x^0; \varepsilon) = L_{j(j-1)}$  or  $U_{j(j-1)}$ . But  $\varepsilon > \varepsilon^0$  implies  $\theta_{(j+1)j} - \varepsilon_{(j+1)j} < L_{j(j-1)}$  and  $U_{j(j-1)} < \theta_{(j+1)j} + \varepsilon_{(j+1)j}$  so that  $\dot{x}_i \neq 0$  at  $x^0$ . Therefore  $x^0$  is not an equilibrium. ■

## 8.2. Proof of Theorem 2

Let  $(Z(s), \varepsilon(s))$  be a smooth parameterization of ramp parameters. We study what happens when a fixed point  $x^0 = x^0(s)$  crosses exactly one threshold  $\theta_{(i+1)i}(s) \pm \varepsilon_{(i+1)i}(s)$  at  $s = s_0$ . We will apply Theorem 2.7 of [Di Bernardo *et al.*, 2008].

Let  $\mu = s - s_0$  and for concreteness assume  $x_N^0(\mu) = \theta_{1N}(\mu) + \varepsilon_{1N}(\mu)$  at  $\mu = 0$ . Near the border, we localize the dynamics of  $\mathcal{R}(Z, \varepsilon)$  as

$$\dot{x} = \begin{cases} F(x, \mu), & x_N \geq \theta_{1N}(\mu) + \varepsilon_{1N}(\mu) \\ G(x, \mu), & x_N < \theta_{1N}(\mu) + \varepsilon_{1N}(\mu). \end{cases} \quad (20)$$

We are only concerned with when an equilibrium crosses a codimension 1 boundary, so  $F$  and  $G$  differ in only one component. Namely, we assume without loss of generality that  $F_j = G_j$  for  $j > 1$ . At the boundary,

the ramp function  $R_1$  has a corner i.e. a discontinuity in the first derivative.  $F$  captures the regime in which  $R_1$  is constant and  $G$  the regime in which  $R_1$  is linear. Explicitly,

$$\begin{aligned} F_1(x, \mu) &= -x_1 + \sigma_{1N}(x_N) \\ G_1(x, \mu) &= -x_1 + \sigma_{1N}(x_N) + s_{1N}m_{1N}(\mu)(x_N - (\theta_{1N}(\mu) + \varepsilon_{1N}(\mu))). \end{aligned}$$

Note that

$$G(x, \mu) - F(x, \mu) = (s_{1N}m_{1N}(\mu))(x_N - (\theta_{1N}(\mu) + \varepsilon_{1N}(\mu)))e_1$$

where  $e_1$  is the unit vector  $(1, 0, \dots, 0)^T$ . In accordance with the notation of the Theorem 2.7 of [Di Bernardo *et al.*, 2008], define  $H(x, \mu) = x_N - (\theta_{1N}(\mu) + \varepsilon_{1N}(\mu))$ ,  $A = F_x$ ,  $B = F_\mu$ ,  $C = H_x$ ,  $D = H_\mu$ , and  $E = (G - F)/H$  all evaluated at  $(x, \mu) = (x^0, 0)$ . Notice that  $A$  is lower bidiagonal and we can compute

$$C = e_N^T, \quad D = \theta'_{1N}(0) + \varepsilon'_{1N}(0), \quad \text{and} \quad E = s_{1N}m_{1N}e_1.$$

To apply the theorem, we need the non-degeneracy conditions

$$\det(A) \neq 0, \quad D - CA^{-1}B \neq 0, \quad \text{and} \quad 1 + CA^{-1}E \neq 0.$$

The first condition holds because  $\det(A) = (-1)^N$ . The second condition expresses that the fixed point meets the boundary with non-zero velocity with respect to  $\mu$  and holds generically. The last condition can also be expressed as  $\det(G_x) \neq 0$  as the following lemma demonstrates.

**Lemma 10.**

$$1 + CA^{-1}E = \frac{\det(G_x)}{\det(A)}.$$

*Proof.* We have  $G = F + EH$  so that

$$G_x = F_x + EH_x = A + EC$$

Define the block matrix

$$M = \begin{pmatrix} A & -E \\ C & 1 \end{pmatrix}.$$

Applying Schur's formula to  $M$  (see, for example, Theorem 1.1 of [Zhang, 2006]) yields

$$\det(A + EC) = \det(A) \det(1 + CA^{-1}E)$$

from which the lemma follows.  $\blacksquare$

Theorem 2.7 of [Di Bernardo *et al.*, 2008] together with Lemma 10 implies that whether the bifurcation is persistent or a non-smooth saddle depends on the relative sign of  $\det(A)$  and  $\det(G_x)$ . By Theorem 2.7 of [Di Bernardo *et al.*, 2008] and Lemma 10, the bifurcation is persistent if  $\det(A)/\det(G_x) > 0$  and a nonsmooth saddle if  $\det(A)/\det(G_x) < 0$ .

First suppose  $x^0 \in \partial\tau(\varepsilon(s_0))$ . We have  $\det(A) = (-1)^N \prod \gamma_j$  and

$$\det(G_x) = (-1)^N \left( \prod_{j=1}^N \gamma_j - M(\varepsilon(s_0)) \right)$$

if  $\mathbf{RN}$  is a positive CFN or

$$\det(G_x) = (-1)^N (1 + M(\varepsilon(s_0)))$$

if  $\mathbf{RN}$  is a negative CFN and  $\Gamma = I$ . This shows that if  $\mathbf{RN}$  is a positive CFN then  $\det(A)/\det(G_x) < 0$  if and only if  $M(\varepsilon(s_0)) > \prod \gamma_j$ . If  $\mathbf{RN}$  is a negative CFN and  $\Gamma = I$  then Proposition 4.11 of [Duncan *et al.*, 2021] shows that  $G_x$  has an eigenvalue with positive real part if and only if  $M(\varepsilon(s_0)) > \sec(\pi/N)^N$  and  $N > 2$ . Now suppose  $x^0 \notin \partial\tau(\varepsilon(s_0))$ . Then  $\det(A) = \det(G_x) = (-1)^N \prod \gamma_j$  so the bifurcation is persistent. Furthermore  $A$  and  $G_x$  both have eigenvalues  $-\gamma_j$  for each  $j = 1, \dots, N$  so the equilibrium is stable on both sides of the bifurcation.

## 9. Discussion

The dynamics for a switching system model of a network are efficiently computable because their structure allows for a combinatorial (finite) analysis which avoids the need for ODE simulation. The DSGRN software package is capable of efficiently computing the dynamics for all parameters in moderate size ( $O(10)$  nodes and edges) networks. We therefore ask if there is a broader class of systems for which these computations can be used to understand their dynamics. Progress was made towards answering this question in [Duncan *et al.*, 2021], where it was shown that these computations can be leveraged to completely understand the equilibria and their stability for a class of a smooth sigmoidal systems as long as the sigmoids are sufficiently steep. In this paper, we study the more restrictive class of ramp systems, whose additional structure allow us to explicitly quantify the required steepness for the equilibrium cells of switching systems to be in one-to-one correspondence with equilibria of ramp systems. To do so, we use the theory of bifurcations in piece-wise smooth systems to characterize the bifurcations that occur as the steepness of the ramp functions are decreased. This bifurcation analysis shows that the stability predicted by the switching system is also guaranteed to be maintained when this steepness requirement is met except when negative loops in the network lead to stabilizing Hopf bifurcations. Finally, we show how to choose a subset of parameters so that the correspondence between switching system equilibrium cells and ramp system equilibria is maintained for the shallowest possible ramp functions when the remaining parameters are fixed.

A natural extension of this work involves questions of non-stationary dynamics. The combinatorial analysis of switching system produces information not only about equilibria, but also about other recurrent dynamics exhibited by the system. We suspect that the existence of periodic orbits, for example, in steep sigmoidal and ramp systems can be inferred from switching system dynamics. Previous work [Gedeon *et al.*, 2017] has shown that there is a close relationship between global switching system dynamics and global dynamics of sigmoidal systems in two dimensional systems. The work on extending this result to higher dimension is in progress. In this context, the characterization of steepness of the ramp functions that preserve global dynamics information from switching system would allow further leveraging of the efficient switching system computations in investigation of network dynamics.

## References

- Cummins, B., Gameiro, M. & Harker, S. [2020] “DSGRN: Dynamic Signatures Generated by Regulatory Networks,” <https://github.com/marciogameiro/DSGRN>.
- Cummins, B., Gedeon, T., Harker, S., Mischaikow, K. & Mok, K. [2016] “Combinatorial representation of parameter space for switching networks,” *SIAM Journal on Applied Dynamical Systems* **15**, 2176–2212.
- de Jong, H. [2002] “Modeling and simulation of genetic regulatory systems: a literature review,” *J Comput Biol* **9**, 67–103, doi:10.1089/10665270252833208.
- Di Bernardo, M., Budd, C. J., Champneys, A. R., Kowalczyk, P., Nordmark, A. B., Tost, G. O. & Piironen, P. T. [2008] “Bifurcations in nonsmooth dynamical systems,” *SIAM review* **50**, 629–701.
- Duncan, W., Gedeon, T., Kokubu, H., Mischaikow, K. & Oka, H. [2021] “Equilibria and their stability in networks with steep sigmoidal nonlinearities,” *arXiv e-prints*, arXiv:2103.17184 URL <https://arxiv.org/abs/2103.17184>.
- Edwards, R. [2001] “Chaos in neural and gene networks with hard switching,” *Diff. Eq. Dyn. Sys.*, 187–220.
- Gardner, T. S., Cantor, C. R. & Collins, J. J. [2000] “Construction of a genetic toggle switch in *escherichia coli*,” *Nature* **403**, 339–342.
- Gedeon, T. [2020] “Multi-parameter exploration of dynamics of regulatory networks,” *Biosystems* **190**, 104113.
- Gedeon, T., Cummins, B., Harker, S. & Mischaikow, K. [2018] “Identifying robust hysteresis in networks,” *PLoS Comput Bio* **14**, e1006121, doi:<https://doi.org/10.1371/journal.pcbi.1006121>.
- Gedeon, T., Harker, S., Kokubu, H., Mischaikow, K. & Oka, H. [2017] “Global dynamics for steep sigmoidal nonlinearities in two dimensions,” *Physica D* **339**, 18–38.
- Gedeon, T. & Mischaikow, K. [1994] “Dynamics of cyclic feedback systems,” *Resenhas do Instituto de Matemática e Estatística da Universidade de São Paulo* **1**, 495–515.

- Glass, L. & Kauffman, S. a. [1973] “The logical analysis of continuous, non-linear biochemical control networks.” *Journal of Theoretical Biology* **39**, 103–29, URL <http://www.ncbi.nlm.nih.gov/pubmed/4741704>.
- Glass, L. & Pasternack, J. S. [1978] “Stable oscillations in mathematical models of biological control systems,” *Journal of Mathematical Biology* **6**, 207–223, URL <http://link.springer.com/article/10.1007/BF02547797>.
- Grossberg, S. [1988] “Nonlinear neural networks: Principles, mechanisms, and architectures,” *Neural Networks* **1**, 17–61.
- Hong, T., Watanabe, K., Ha Ta, C., Villarreal-Ponce, A., Nie, Q. & Dai, X. [2015] “An Ovol2-Zeb1 mutual inhibitory circuit governs bidirectional and multi-step transition between epithelial and mesenchymal states,” *PLoS Comput Biol* **11**, e1004569, doi:10.1371/journal.pcbi.1004569.
- Hopfield, J. [1982] “Neural networks and physical systems with emergent collective computational abilities,” *Proceedings of the National Academy of Sciences of the USA* **79**, 2554–2558.
- Ironi, L., Panzeri, L., Plahte, E. & Simoncini, V. [2011] “Dynamics of actively regulated gene networks,” *Physica D: Nonlinear Phenomena* **240**, 779–794, doi:10.1016/j.physd.2010.12.010, URL <http://linkinghub.elsevier.com/retrieve/pii/S016727891000360X>.
- Jaeger, H. & Haas, H. [2004] “Harnessing nonlinearity: Predicting chaotic systems and saving energy in wireless communication,” *Science* **304**, 78–80, doi:10.1126/science.1091277, URL <https://science.sciencemag.org/content/304/5667/78>.
- Jolly, M., Tripathi, S., Jia, D., Mooney, S., Celiktas, M., Hanash, S., Mani, S., Pienta, K., Ben-Jacob, E. & Levine, H. [2016] “Stability of the hybrid epithelial/mesenchymal phenotype,” *Oncotarget* **10:7**, 27067–84, doi:10.18632/oncotarget.8166.
- Thomas, R. [1991] “Regulatory networks seen as asynchronous automata: A logical description,” *Journal of Theoretical Biology* **153**, 1–23, doi:10.1016/S0022-5193(05)80350-9.
- Veflingstad, S. R. & Plahte, E. [2007] “Analysis of gene regulatory network models with graded and binary transcriptional responses,” *Biosystems* **90**, 323–339.
- Xin, Y., Cummins, B. & Gedeon, T. [2020] “Multistability in the epithelial-mesenchymal transition network,” *BMC Bioinformatics* **21**, 1–17.
- Zhang, F. [2006] *The Schur complement and its applications*, Vol. 4 (Springer Science & Business Media).