Regulatory dynamics on random networks: asymptotic periodicity and modularity

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Abstract
We study the dynamics of discrete-time regulatory networks on random digraphs. For this we define ensembles of deterministic orbits of random regulatory networks, and introduce some statistical indicators related to the long-term dynamics of the system. We prove that, in a random regulatory network, initial conditions almost certainly converge to a periodic attractor. We study the subnetworks, which we call modules, where the periodic asymptotic oscillations are concentrated. We prove that those modules are dynamically equivalent to independent regulatory networks.

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(Some figures in this article are in colour only in the electronic version)

1. Introduction
Numerous natural and artificial systems can be thought of as a collection of basic units interacting according to simple rules. Examples of these interacting systems are the genetic regulatory networks, composed of interactions between DNA, RNA, proteins and small molecules. In social or ecological networks, similar regulatory dynamics may also be considered. The traditional way to model these systems is by using coupled differential equations, and more particularly systems of piecewise affine differential equations (see [6,7,9,17]). Finite state models, better known as logical networks, are also used (see [11,13,19]). Within these modelling strategies, the interacting units have a regular behaviour when taken separately, but are capable of generating global complex dynamics when arranged in a complex interaction architecture. In all the models considered so far, each interacting unit regulates some other units in the collection by enhancing or repressing their activity. It is possible then to define an underlying network with interacting units as vertices, and their interactions as arrows connecting those vertices. The theoretical problem
we face here is to understand the relation between the structure of the underlying network and the possible dynamical behaviours of the system. We will do this in the context of a particular class of models first introduced in [22] and further studied in [5] and [16]. In these models, the level of activity of each unit is codified by a positive real number. The system evolves synchronously at discrete time steps, each unit following an affine contraction dictated by the activity level and interaction mode of its neighbouring units. The contraction coefficient of those transformations determines the degradation rate at which, in the absence of interactions, the activity of a given unit vanishes. In the framework of this modelling we have proved general results concerning the constraints imposed by the structure of the underlying network, over the possible asymptotic behaviours of a fixed system [16]. In this paper, following [22], we will focus on the asymptotic dynamics of regulatory systems whose interactions are chosen at random at the beginning of the evolution. Within this approach, individual orbits are elements of a sample space, and the statistical indicators we will study become orbit dependent random variables. The probability measures we used are built from a fixed probability distribution over the set of possible underlying networks. Then, given a fixed underlying network, we associate a sign to each one of its arrows, depending on whether the interaction they represent are activations or inhibitions. Positive and negative signs are randomly chosen, keeping a fixed proportion of negative arrows inside a given statistical ensemble of systems. In this way it is possible to study certain characteristics of the asymptotic dynamics, as a function of the degradation rate and the proportion of inhibitory interactions.

Our first result states that in a random regulatory network, initial conditions almost certainly converge to a periodic attractor. This result points to the conclusion that in regulatory dynamics, the origin of the complexity is the coexistence of multiple dynamically simple attractors. We prove that this is the case in a full measure set in the parameter space.

According to our preliminary numerical explorations, the long-term oscillations of the system concentrate on a subnetwork whose structure depends on the parameters of the statistical ensemble of regulatory networks. Our second result states that the dynamics one can observe when restricted to the oscillatory subnetwork is equivalent to the dynamics supported by the subnetwork considered as an isolated system. This result allows us to introduce the concept of modularity. If we call module any observable oscillatory subnetwork, then, according to our result, the dynamics of a small network is preserved when it appears as a module in a larger network. We interpret this as the emergence of modularity. This result allows us to predict admissible asymptotic behaviours in regulatory networks admitting disconnected oscillatory subnetworks. It is worth mentioning that this kind of modularity was already studied in the context of Boolean networks [3] and more recently in continuous-time regulatory networks [10]. Our approach allows a formal approach to the problems addressed in those works.

The paper is organized as follows. In the next section we will introduce the objects under study, then in section 3 we will state the results and present some of the proofs. After reviewing two examples, which we do in section 4, we will give the proofs of the two more technical results in section 5. The paper ends with a section of final comments and conclusions.

2. Preliminaries

2.1. Regulatory networks as dynamical systems

The interaction architecture of the regulatory network is encoded in a directed graph \( G = (V, A) \), where vertices \( V \) represent interacting units, and the arrows \( A \subseteq V \times V \) denote interaction between them. With each interaction \((u, v) \in A\) we associate a threshold.
\( T_{(u,v)} \in [0, 1] \) and a sign \( \sigma_{(u,v)} \in \{-1, 1\} \) that is chosen according to whether this interaction is an inhibition or an activation. We quantify the activity of each unit \( v \in V \) with real number \( x_v \in [0, 1] \). Thus, the activation state of the network at a given time \( t \) is determined by the vector \( x^t \in [0, 1]^V \). The influence of a unit \( u \) over a target unit \( v \) turns on or off, depending on its sign, when the value of \( x_u \) trespasses the threshold \( T_{(u,v)} \). The evolution of the network is generated by the iteration of the map \( F_{\sigma,T} : [0, 1]^V \to [0, 1]^V \) such that

\[
 x^{t+1} = F_{\sigma,T}(x^t) := ax^t + (1-a)\vartheta(x^t),
\]

where the contraction rate \( a \in [0, 1] \) determines the speed of degradation of the activity of the units in the absence of interaction, and the interaction term \( D_{\sigma,T} : [0, 1]^V \to [0, 1]^V \) is the piecewise constant function defined by

\[
 D_{\sigma,T}(x) := \frac{1}{\text{Id}(x)} \sum_{(u,v) \in A} H(\sigma_{(u,v)}(x_u - T_{(u,v)})).
\]

Here \( H : \mathbb{R} \to \mathbb{R} \) is the Heaviside function and \( \text{Id}(x) := \#\{u \in V : (u, v) \in A\} \) stands for the input degree of the vertex. We will be referring to the discontinuity set of the transformation \( F_{\sigma,T} \), which is

\[
 \Delta_T := \{ x \in [0, 1]^V : x_u = T_{(u,v)} \text{ for some } (u, v) \in A \}.
\]

For each \( a \in [0, 1] \), the transformation \( F_{\sigma,T} \) is a piecewise affine contraction with discontinuity set \( \Delta_T \).

From now on, by a discrete-time regulatory network we will mean a discrete-time dynamical system \( (\mathbb{R}^1)^V, F_{\sigma,T} \), with phase space \( \mathbb{R}^1 \), and evolution generated by the piecewise affine contraction \( F_{\sigma,T} : [0, 1]^V \to [0, 1]^V \) defined in equation (1). The discrete-time regulatory networks studied here have interactions of equal strength, and they act additively on each target unit. More general discrete-time regulatory networks have been considered in [5, 16].

2.2. Statistical ensembles

We build our statistical ensembles as follows. We fix the value of the contraction rate \( a \in [0, 1] \) and the set \( V \) representing the interacting units. Then we consider the set of all possible piecewise transformations,

\[
 \mathcal{F}_{a,V} := \{ F_{\sigma,T} : \mathcal{G} := (V, A), \sigma \in \{-1, 1\}^A, T \in [0, 1]^A \}.
\]

The individual elements of our statistical ensembles are couples \( (F_{\sigma,T}(x), x) \), with \( F_{\sigma,T} \in \mathcal{F}_{a,V} \) and \( x \in [0, 1]^V \). A couple \( (F_{\sigma,T}(x), x) \) determines a deterministic orbit \( \{ x^t \} \) such that

\[
 \mathbb{P}_{a,V}(\cdot) = \mathbb{P}_{\mathcal{G}}(\cdot) \times \mathbb{P}_{A,\eta}(\cdot) \times \text{vol}(\mathcal{I}) \times \text{vol}(\mathcal{J}),
\]

for all rectangles \( \mathcal{I} \subset [0, 1]^A \) and \( \mathcal{J} \subset [0, 1]^V \). Here \( \mathbb{P}_{A,\eta} : \{-1, 1\}^A \to [0, 1] \) is such that

\[
 \mathbb{P}_{A,\eta}(\sigma) = \prod_{(u,v) \in A} \left( \frac{\sigma_{(u,v)} + 1}{2} - \frac{\sigma_{(u,v)} \eta}{2} \right),
\]

and \( \text{vol} \) stands for the Lebesgue measure on the corresponding euclidean spaces.
2.3. Some graph-theoretical notations and definitions

A path in $\mathcal{G} = (A, V)$ is a sequence $u_0, u_1, \ldots, u_k$, with $u_i \in V$ and $(u_i, u_{i+1}) \in A$ for each $i$. The length of a path is the number of arrows it contains. A cycle is a path $u_0, u_1, \ldots, u_k$, where $u_0 = u_k$. We say that the vertices $u, v \in V$ are connected if there exists a cycle $u_0, u_1, \ldots, u_k$ such that $u, v \in \{u_0, u_1, \ldots, u_k\}$. The connected components of $\mathcal{G}$ are the maximal subgraphs of $\mathcal{G}$ such that all their vertices are connected. The distance between two vertices $u, v \in V$, which we denote $d_G(u, v)$, is the length of the shortest directed path whose end vertices are $u$ and $v$.

2.4. The oscillatory subnetwork and the asymptotic period

With each couple $(F_{0, \sigma, T, a}, x)$ we associate a directed graph $\mathcal{G}_{osc} := (\mathcal{V}_{osc}, A_{osc}) \subseteq \mathcal{G}$, the oscillatory subnetwork, defined by

$$A_{osc} := \{(u, v) \in A : H(x_u - T_{a,v}) \text{ does not converge}\},$$

$$\mathcal{V}_{osc} := \{v \in V : \exists u \in V \text{ such that } \{(u, v), (v, u)\} \cap A_{osc} \neq \emptyset\}.$$

By definition, the oscillatory subnetwork is spanned by all the arrows whose activation state $H(\sigma_u(x_u - T_{a,v}))$ changes infinitely often. This subnetwork is the equivalent, in discrete-time regulatory networks, to the dynamical islands introduced in [10] for continuous-time regulatory networks. They are also related to the clusters of relevant elements in Boolean networks, as they were defined in [3]. Unlike the differential equations and the finite state modelling strategies of regulatory dynamics [14, 20, 21], our models admit oscillations in all network topologies, regardless of the distribution of activations and inhibitions through the graph. This is possible because of the discreteness of time and continuity of the state variable. Therefore, oscillatory subnetworks may occur in any discrete-time regulatory network.

The oscillatory subnetwork can be seen as a random variable

$$\mathcal{G}_{osc} : \mathcal{F}_{a,V} \times [0, 1]^V \to \Theta_{\subseteq V} := \{V \subseteq V : V \subset \tilde{V} \subset \tilde{V} \subset V\},$$

from which we can derive other statistical indicators, as for instance its size $\#\mathcal{V}_{osc}$, the number $nc(\mathcal{G}_{osc})$ of its connected components and its degree distribution

$$\rho_{\mathcal{G}_{osc}}(k) := \frac{\#\{v \in \mathcal{V}_{osc} : \text{Id}_{\mathcal{G}_{osc}}(v) = k\}}{\#\mathcal{V}_{osc}},$$

where $\text{Id}_{\mathcal{G}_{osc}}(v) := \{u \in \mathcal{V}_{osc} : (u, v) \in A_{osc}\}$.

Another statistical indicator we will consider is the asymptotic period of a given orbit. Denote by $\text{Per}_t(F_{G, \sigma, T, a})$ the set of all $F_{G, \sigma, T, a}$-periodic points of minimal period $\tau$, i.e.

$$\text{Per}_t(F_{G, \sigma, T, a}) = \{x \in [0, 1]^V : F^t_{G, \sigma, T,a}(x) = x \text{ and } F^t_{G, \sigma, T,a}(x) \neq x \text{ if } t < \tau\}.$$  \hspace{1cm} (7)

We will say that the asymptotic $F_{G, \sigma, T, a}$-period of $x \in [0, 1]^V$ is $\tau$ if there exists $y \in \text{Per}_t(F_{G, \sigma, T, a})$, such that

$$\lim_{t \to \infty} |F^t_{G, \sigma, T,a}(x) - F^t_{G, \sigma, T,a}(y)| = 0.$$

We will denote this by $P(F_{G, \sigma, T, a}, x) = \tau$.

3. Results

3.1. The asymptotic period

With each finite set $V$, and $a \in [0, 1)$, we associate the sample space $\mathcal{F}_{a,V} \times [0, 1]^V$, with $\mathcal{F}_{a,V}$ as in equation (4). We supply this sample space with the product sigma-algebra, taking
for $[0, 1]^V$ and $[0, 1]^A$, the corresponding Borel sigma-algebras. The next result concerns the asymptotic period $(F\bar{a},\sigma,T,a,x) \mapsto P(F\bar{a},\sigma,T,a,x)$.

**Theorem 1.** Given a finite set $V$, and $a \in [0, 1)$, the function $P : F_{a,V} \times [0, 1]^V \to \mathbb{N}$ which assigns to $(F\bar{a},\sigma,T,a,x) \in F_{a,V} \times [0, 1]^V$ the value of the asymptotic $F\bar{a},\sigma,T,a$-period of $x$ is a measurable function. Furthermore, for each $\eta \in [0, 1]$,

$$\mathbb{P}_{a,\eta}(F\bar{a},\sigma,T,a,x) \in F_{a,V} \times [0, 1]^V : P(F\bar{a},\sigma,T,a,x) < \infty) = 1.$$ 

This expected but nontrivial result says that a random orbit will almost certainly approach a periodic orbit; otherwise said, an initial condition almost certainly converges to a periodic attractor. It is because of this result that we can restrict ourselves to the study of periodic orbits, even though the parameter set for which the orbits are infinite may be uncountable (see [5]). We could therefore redefine the oscillatory subnetwork by saying that, after a transitory state, their arrows periodically change their activation state. The proof of this result and some related comments are left to section 5.1.

### 3.2. Modularity

In this paragraph we will consider probability measures obtained by conditioning on a subnetwork from a given statistical ensemble of regulatory networks. Given $\mathbb{P}_{a,\eta}$ on $F_{a,V} \times [0, 1]^V$, and a subnetwork $\bar{G} := (\bar{V}, \bar{A}) \in \bar{G}_{\subset V}$, we define the analogous probability measure $\mathbb{P}_{a,\eta,\bar{G}}$ on $F_{a,\bar{V}} \times [0, 1]^\bar{V}$, such that

$$\mathbb{P}_{a,\eta,\bar{G}}(F_{\bar{a},\bar{\sigma},\bar{T},\bar{a},\bar{x}, \bar{y}) : \bar{T} \in \bar{I}, \bar{y} \in \bar{J}) := \begin{cases} \mathbb{P}_{a,\eta}(\bar{\sigma}) \text{ vol} (\bar{I}) \text{ vol} (\bar{J}) & \text{if } \bar{G} = \bar{G}, \\ 0 & \text{otherwise}, \end{cases}$$

for each $\bar{\sigma} \in \{-1, 1\}^\bar{A}$, and all rectangles $\bar{I} \subset [0, 1]^{\bar{A}}$ and $\bar{J} \subset [0, 1]^{\bar{V}}$. As before, vol denotes the corresponding Lebesgue measures. This measure can also be seen as the marginal of $\mathbb{P}_{a,V}$ obtained by projecting over $\bar{V} \subset V$, then conditioned to have the underlying network $\bar{G} \in \bar{G}_{\subset V}$.

**Theorem 2.** Fix $a \in [0, 1)$, $\eta \in [0, 1]$, and a digraph $\bar{G} = (\bar{V}, \bar{A}) \in \bar{G}_{\subset V}$ with $\bar{V} \subset V$. If the digraph distribution $\mathbb{P}_{\bar{G}}$ is such that $\mathbb{P}_{\bar{G}}(\bar{G}) > 0$ for all $\bar{G} \in \bar{G}_{\subset V}$, and if $\mathbb{P}_{a,\eta} (\text{osc} = \bar{G}) > 0$, then we can associate with $\bar{G}$:

(a) a digraph extension $\bar{G}_{\text{ext}} := (V, A) \in \bar{G}_{\subset V},$
(b) rectangles $\bar{I} := \bar{I} \times I' \subset [0, 1]^\bar{A} \times [0, 1]^A$ and $\bar{J} := \bar{J} \times J' \subset [0, 1]^{\bar{V}} \times [0, 1]^{V \setminus \bar{V}}$,
(c) and for each $\bar{\sigma} \in \{-1, 1\}^\bar{A}$, an extension $\bar{\sigma}_{\text{ext}} \in \{-1, 1\}^A$ such that $\bar{\sigma}_{\text{ext}}|_{\bar{A}} = \bar{\sigma}$.

These associated objects satisfy $\text{osc}(F_{\bar{a},\bar{\sigma}_{\text{ext}},T,a,x}) \subset \bar{G} \forall T \in I, x \in \mathcal{J},$ and $\bar{\sigma} \in \{-1, 1\}^\bar{A}$.

Furthermore, $G_{\text{ext}}$, $I$ and $\mathcal{J}$ define surjective transformations

(d) $\Phi_A : \bar{I} \times I' \to [0, 1]^A$, such that $\Phi_A(\bar{T} \times T') = D_{\bar{A}} \bar{T} + C_{\bar{A}}$ with $D_{\bar{A}}$ diagonal and $C_{\bar{A}}$ constant,
(e) and similarly, $\Phi_V : \bar{J} \times J' \to [0, 1]^V$ such that $\Phi_V(\bar{x} \times x') = D_{\bar{V}} \bar{x} + C_{\bar{V}}$, with $D_{\bar{V}}$ diagonal and $C_{\bar{V}}$ constant.

These transformations satisfy

$$\Phi_V \circ F_{\bar{a},\bar{\sigma}_{\text{ext}},T,a}(x) = F_{\bar{a},\bar{\sigma}_{\text{ext}},\Phi_A(T),a} \circ \Phi_V(x),$$

for all $T \in I$, and $x \in \mathcal{J}$. 

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The proof of this result follows from a construction, and it is postponed to section 5. Let us now expose its interpretation and some of its consequences. We can divide this theorem into two parts, the first part concerns the stability of the oscillatory subnetworks. It says that if an oscillatory subnetwork $\tilde{G} := (\tilde{V}, \tilde{A})$ has a positive probability of occurring, then to each signs matrix $\tilde{\sigma} \in \{-1, 1\}^A$ it corresponds an oscillatory subnetwork which is a subgraph of $\tilde{G}$. Furthermore, the set of initial conditions and thresholds for which a given subgraph of $\tilde{G}$ is the oscillatory subnetwork is a rectangle with nonempty interior. Therefore, each of those subgraphs is stable under small changes in the thresholds $T \in [0, 1]^A$, and in the initial condition $x \in [0, 1]^V$. The size of the maximal perturbation depends on the position of $(T, x)$ with respect to the borders of the above-mentioned rectangle.

More interestingly, the second part of the theorem states that if an oscillatory subnetwork has a positive probability of occurring, then the dynamics one can observe when restricted to that subnetwork is equivalent to the dynamics supported by the subnetwork considered as an isolated system. The equivalence is achieved through the transformation $\Phi_A$ and $\Phi_V$. It is because of this equivalence that we can talk about modularity. Indeed, if we call module any oscillatory subnetwork occurring with positive probability, then this theorem can be rephrased by saying that each orbit admissible in a module considered as an isolated system can be achieved, up to a change of variables, as the restriction of an orbit in the original system. The network extension $\tilde{G}_{\text{ext}}$, the values of the external thresholds $T' \in [0, 1]^{\tilde{V}}$, and the external initial conditions $\tilde{x}' \in [0, 1]^{\tilde{V}}$ can be thought of as analogous in our systems to the functionality context defined in [18] for logical networks. Using their nomenclature, our theorem ensures that if an oscillatory subnetwork has a positive probability of occurring, then there is a positive measure set of contexts making this subnetwork functional.

An interesting consequence of the previous theorem is the following corollary.

**Corollary 1.** Fix $a \in [0, 1)$, $\eta \in [0, 1]$ and $G := G_1 \cup G_2 \in \mathfrak{G}_\leq V$, with $G_1 := (V_1, A_1)$ and $G_2 := (V_2, A_2)$ vertex disjoint and such that $V_1 \cup V_2 \subseteq V$. If the digraph distribution $P_G$ is such that $P_G(G) > 0$ for all $G \in \mathfrak{G}_V$, and if $P_{a, \eta}(G_{\text{osc}} \subseteq \tilde{G}) > 0$, then

$$P_{a, \eta}(P = \tau) \geq C \sum_{\text{lcm}(\tau_1, \tau_2) = \tau} P_{a, \eta, G_1}(P = \tau_1) \times P_{a, \eta, G_2}(P = \tau_2),$$

with $C > 0$ a constant depending on $P_{a, \eta}$ and $\tilde{G}$.

The probabilities in the sum at the right hand side of the inequality are analogous probability measures of the kind defined by equation (8). They are obtained as marginal probabilities corresponding to projections over the vertex sets $V_1$ and $V_2$, then conditioned to have underlying network $G_1$ and $G_2$, respectively.

In [3] the authors study the relationship between the modular structure and the periods distribution in Boolean networks. The previous corollary establishes such a relation in the framework of discrete-time regular networks. Our result relates the distribution of the asymptotic period of a network $G$ to the distribution of the asymptotic period of its oscillatory subnetworks considered as isolated systems. It establishes, in particular, that the observable asymptotic periods of $G$ are the least common multiples of the observable asymptotic periods of its oscillatory subnetworks.

**Proof.** First notice that for each $\tilde{G} \in \mathfrak{G}_\leq V$, we have

$$P_{a, \eta}(P = \tau) \geq P_{a, \eta}(P = \tau | G_{\text{osc}} \subseteq \tilde{G}) \times P_{a, \eta}(G_{\text{osc}} \subseteq \tilde{G}).$$

Let $\tilde{G} := (\tilde{V}, \tilde{A}) = (V_1 \cup V_2, A_1 \cup A_2)$, with $G_1 := (V_1, A_1)$ and $G_2 := (V_2, A_2)$ vertex disjoint. Theorem 2 ensures the existence of the following objects associated with $\tilde{G}$: (a) the extension $\tilde{G}_{\text{ext}} := (\tilde{V}, A) \in \mathfrak{G}_V$ such that $\tilde{G} \subseteq \tilde{G}_{\text{ext}}$, (b) two affine surjective transformations $\Phi_A: \mathcal{I} \to [0, 1]^{A_1}$, $[0, 1]^{A_2}$ and $\Phi_V: \mathcal{J} \to [0, 1]^{V_1} \times [0, 1]^{V_2}$.
and (c) for each $\tilde{\sigma} \equiv \tilde{\sigma}^{(1)} \times \tilde{\sigma}^{(2)} \in \{-1, 1\}^{A_1} \times \{-1, 1\}^{A_2}$, an extension $\tilde{\sigma}_{\text{ext}} \in \{-1, 1\}^{A}$ such that $\sigma|_{A_1 \cup A_2} \equiv \tilde{\sigma}$. From the second part of the theorem it follows that

$$\Phi_V(F^i_{\text{ext}, \tilde{\sigma}_{\text{ext}}, TT, a}(x)) = F^i_{\tilde{\sigma}^{(1)}, T^{\tilde{\sigma}^{(2)}}, \tilde{\sigma}^{(1)}, \tilde{\sigma}^{(2)}, a}(y^{(1)}) \times F^i_{\tilde{\sigma}^{(1)}, T^{\tilde{\sigma}^{(2)}}, \tilde{\sigma}^{(1)}, \tilde{\sigma}^{(2)}, a}(y^{(2)}),$$

(9)

for all $i \in \mathbb{N}$ and $(T, x) \in \mathcal{I} \times \mathcal{J}$. Here we have used $\Phi_V(T) \equiv \tilde{T}^{(1)} \times \tilde{T}^{(2)} \in [0, 1]^{A_1} \times [0, 1]^{A_2}$ and $\Phi_V(x) \equiv y^{(1)} \times y^{(2)} \in [0, 1]^{\mathcal{V}_1} \times [0, 1]^{\mathcal{V}_2}$. For $i = 1, 2$ and each $\tilde{\sigma}^{(i)} \in \{-1, 1\}^{A_i}$ and $\tau_i \in \mathbb{N}$, let us define

$$P_{\tilde{\sigma}^{(1)}, \tilde{\sigma}^{(2)}, \tau_i} := \{(\tilde{T}^{(i)}, y^{(i)}) \in [0, 1]^{A_i} \times [0, 1]^{\mathcal{V}_i} : P(F_{\tilde{\sigma}^{(1)}, \tilde{\sigma}^{(2)}, \tau_i}, y^{(i)}) = \tau_i\}.$$

Defining $\Phi : \mathcal{I} \times \mathcal{J} \to [0, 1]^{A} \times [0, 1]^{\mathcal{V}}$ such that $\Phi(T, x) \equiv \Phi_A(T) \times \Phi_V(x)$, it follows from (9) that

$$\mathbb{P}_{\tilde{G}, \eta}(P = \tau | G_{\text{osc}} \subseteq \tilde{G}) \geq \frac{\mathbb{P}_G(G_{\text{ext}})}{|\mathcal{D}| \mathbb{P}_{\tilde{G}, \eta}(G_{\text{osc}} \subseteq \tilde{G})} \sum_{\tilde{\sigma} \equiv \tilde{\sigma}^{(1)} \times \tilde{\sigma}^{(2)}} \mathbb{P}_{A_{\tilde{\sigma}}}(\tilde{\sigma}_{\text{ext}})
\times \sum_{\text{lcm}(\tau_1, \tau_2) = \tau} \text{vol} \circ \Phi^{-1}(P_{\tilde{\sigma}^{(1)}, \tilde{\sigma}^{(2)}, \tau_1} \times P_{\tilde{\sigma}^{(1)}, \tilde{\sigma}^{(2)}, \tau_2}),$$

where $\text{vol}$ denotes Lebesgue measure in $[0, 1]^{A} \times [0, 1]^{\mathcal{V}}$. Let us now use the decomposition $\mathcal{I} = \mathcal{I} \times \mathcal{J} \subset [0, 1]^{A} \times [0, 1]^{A_1}$ and $\mathcal{J} = \mathcal{J} \times \mathcal{J} \subset [0, 1]^{\mathcal{V}_1} \times [0, 1]^{\mathcal{V}_1}$. According to theorem 2, we have

$$\Phi((\tilde{T} \times T') \times (\tilde{x} \times x')) = D(\tilde{T} \times \tilde{x}) + \mathcal{C},$$

where $D$ is a diagonal linear bijection and $\mathcal{C}$ is a constant. With this,

$$\mathbb{P}_{\tilde{G}, \eta}(P = \tau | G_{\text{osc}} \subseteq \tilde{G}) \geq \frac{\mathbb{P}_G(G_{\text{ext}})}{|\mathcal{D}| \mathbb{P}_{\tilde{G}, \eta}(G_{\text{osc}} \subseteq \tilde{G})} \sum_{\tilde{\sigma} \equiv \tilde{\sigma}^{(1)} \times \tilde{\sigma}^{(2)}} \mathbb{P}_{A_{\tilde{\sigma}}}(\tilde{\sigma}_{\text{ext}})
\times \sum_{\text{lcm}(\tau_1, \tau_2) = \tau} \text{vol}_1(P_{\tilde{\sigma}^{(1)}, \tilde{\sigma}^{(2)}, \tau_1}) \times \text{vol}_2(P_{\tilde{\sigma}^{(1)}, \tilde{\sigma}^{(2)}, \tau_2}),$$

where $\text{vol}$ denotes the Lebesgue measure in $[0, 1]^{A} \times [0, 1]^{\mathcal{V}}$, $\text{vol}_i$ denotes the Lebesgue measure in $[0, 1]^{A_i} \times [0, 1]^{\mathcal{V}_i}$ for $i = 1, 2$ and $|\mathcal{D}|$ denotes the determinant of the transformation $D$. From here, and taking into account the definition in equation (8), we have

$$\mathbb{P}_{\tilde{G}, \eta}(P = \tau | G_{\text{osc}} \subseteq \tilde{G}) \geq \frac{\mathbb{P}_G(G_{\text{ext}})}{|\mathcal{D}| \mathbb{P}_{\tilde{G}, \eta}(G_{\text{osc}} \subseteq \tilde{G})} \times \sum_{\tilde{\sigma} \equiv \tilde{\sigma}^{(1)} \times \tilde{\sigma}^{(2)}} \mathbb{P}_{A_{\tilde{\sigma}}}(\tilde{\sigma}^{(1)}) \times \mathbb{P}_{A_{\tilde{\sigma}}}(\tilde{\sigma}^{(2)})
\times \sum_{\text{lcm}(\tau_1, \tau_2) = \tau} \text{vol}_1(P_{\tilde{\sigma}^{(1)}, \tilde{\sigma}^{(2)}, \tau_1}) \times \text{vol}_2(P_{\tilde{\sigma}^{(1)}, \tilde{\sigma}^{(2)}, \tau_2})
\geq \frac{\mathbb{P}_G(G_{\text{ext}})}{|\mathcal{D}| \mathbb{P}_{\tilde{G}, \eta}(G_{\text{osc}} \subseteq \tilde{G})} \times \sum_{\text{lcm}(\tau_1, \tau_2) = \tau} \mathbb{P}_{A_{\tilde{\sigma}}}(P = \tau_1) \mathbb{P}_{A_{\tilde{\sigma}}}(P = \tau_2),$$

and the result follows with $C := \mathbb{P}_G(G_{\text{ext}}) \times \text{vol}(\mathcal{I} \times \mathcal{J}) \times \min(\eta, 1 - \eta)^{\mathcal{V}/|\mathcal{D}|}$. □
3.3. Sign symmetry

The next result illustrates how a structural constraint in the underlying random network manifests in the distribution of the statistical indicators. Here, the fact that the underlying random digraph does not admit cycles of odd length implies a symmetry on the statistical indicators with respect to the change of sign in the interactions. Let us recall that for each \( \eta \in [0, 1] \) and \( a \in [0, 1) \), the probability measure \( \mathbb{P}_{a,\eta} \) on \( \mathcal{F}_{a,V} \times [0, 1]^V \) which defines a statistical ensemble is obtained from a fixed distribution \( \mathbb{P}_G \) over the finite set of all directed graphs with vertices in \( V \). We have the following proposition.

**Proposition 1.** If the distribution \( \mathbb{P}_G \) over the set \( \mathcal{G}_V \) of all directed graphs with vertices in \( V \) is such that \( \mathbb{P}_G \{ G \in \mathcal{G}_V : G \text{ admits a cycle of odd length} \} = 0 \), then

\[
\mathbb{P}_{a,\eta}(\mathbb{P} = \tau) = \mathbb{P}_{a,1-\eta}(\mathbb{P} = \tau), \quad \forall \tau \in \mathbb{N},
\]

\[
\mathbb{P}_{a,\eta}(G_{osc} = \tilde{G}) = \mathbb{P}_{a,1-\eta}(G_{osc} = \tilde{G}), \quad \forall \tilde{G} \in \mathcal{G}_V,
\]

for each \( \eta \in [0, 1] \).

Statistical ensembles of regulatory networks whose underlying digraphs are random trees (as defined in section 4.1) clearly satisfy the hypothesis of proposition 1. Random subnetworks of the square lattice also have this property. Therefore, for regulatory dynamics over those kinds of digraphs, the statistical indicators we consider are left invariant under the symmetry \( \eta \mapsto 1 - \eta \).

In the proof of proposition 1, we will need the following lemma.

**Lemma 1.** For each \( G := (V, A) \in \mathcal{G}_V \), and \( \sigma \in \{-1, 1\}^A \) we have

\[
\text{vol} \left( (T, x) \in [0, 1]^A \times [0, 1]^V : \{ F^t_{G,\sigma,T,a}(x) : t \in \mathbb{N} \} \cap \Delta_T = \emptyset \right) = 1,
\]

where \( \Delta_T := \{ x \in [0, 1]^V : x_u = T_{u,v} \text{ for some } (u, v) \in A \} \) is the discontinuity set of the piecewise constant part of \( F_{G,\sigma,T,a} \).

This lemma follows directly from the arguments developed below, in paragraphs 5.1.3 and 5.1.4, inside the proof of theorem 1.

**Proof of proposition 1.** First notice that for each \( G = (A, V) \in \mathcal{G}_V \) and \( \sigma \in \{-1, 1\}^A \) we have

\[
\mathbb{P}_{A,1-\eta}(-\sigma) = \prod_{(u,v) \in A} \left( \frac{-\sigma_{(u,v)} + 1}{2} + \sigma_{(u,v)}(1 - \eta) \right)
\]

\[
= \prod_{(u,v) \in A} \left( \frac{\sigma_{(u,v)} + 1}{2} - \sigma_{(u,v)}\eta \right) = \mathbb{P}_{A,\eta}(\sigma).
\]

Let us suppose that all the cycles in \( G \) have even length and for each connected component of \( \tilde{G} := (\tilde{A}, \tilde{V}) \subseteq G = (A, V) \in \mathcal{G}_V \) choose a pivot vertex \( \tilde{u} \in \tilde{V} \). With this define \( \Psi_A : [0, 1]^A \to [0, 1]^A \) and \( \Psi_V : [0, 1]^V \to [0, 1]^V \) such that

\[
\Psi_A(T_{(u,v)}) := \begin{cases} 1 - T_{(u,v)} & \text{if } d_G(u, \tilde{u}) \in 2\mathbb{N} \\ T_{(u,v)} & \text{otherwise} \end{cases} \quad \Psi_V(x)_u := \begin{cases} 1 - x_u & \text{if } d_G(u, \tilde{u}) \in 2\mathbb{N} \\ x_u & \text{otherwise} \end{cases}
\]

for each \( u, v \in \tilde{V} \). Here \( d_G \) denotes vertex distance induced by the digraph \( G \), as defined in section 2.3. Both \( \Psi_A \) and \( \Psi_V \) are affine isometries, therefore they preserve the Lebesgue...
measure in \([0, 1]^4\) and \([0, 1]^V\), respectively. If \(d_p(v, \bar{u})\) is even, then \(\Psi_V(x)_v = 1 - x_v\), and for each \(u\) such that \((u, v) \in A\), \(\Psi_A(x)_u = x_u\) and \(\Psi_A(T)(u, v) = T(u, v)\). In this case we have

\[
F_{\bar{G}, -\sigma, \Psi_A(T), a}(\Psi_V(x))_v = a(1 - x_v) + \frac{1 - a}{\text{Id}(v)} \sum_{u \in \Psi^{-1}(0, v) \in A} H(-\sigma(u,v)(x_u - T(u, v)))
\]

\[
= a(1 - x_v) + \frac{1 - a}{\text{Id}(v)} \sum_{u \in \Psi^{-1}(0, v) \in A} (1 - H(\sigma(u,v)(x_u - T(u, v))))
\]

\[
= 1 - F_{\bar{G}, -\sigma, \Psi_A(T), a}(x)_v = \Psi_V(F_{\bar{G}, -\sigma, \Psi_A(T), a}(x))_v,
\]

for each \(x \notin \Delta_T\). On the other hand, if \(d_p(v, v_{\text{pivot}})\) is odd, we have \(\Psi_V(x)_v = x_v\), and for each \(u\) such that \((u, v) \in A\), \(\Psi_A(x)_u = 1 - x_u\) and \(\Psi_A(T)(u, v) = 1 - T(u, v)\). In this case

\[
F_{\bar{G}, -\sigma, \Psi_A(T), a}(\Psi_V(x))_v = ax_v + \frac{1 - a}{\text{Id}(v)} \sum_{u \in \Psi^{-1}(0, v) \in A} H(-\sigma(u,v)(x_u - (1 - T(u, v))))
\]

\[
= ax_v + \frac{1 - a}{\text{Id}(v)} \sum_{u \in \Psi^{-1}(0, v) \in A} H(\sigma(u,v)(x_u - T(u, v)))
\]

\[
= F_{\bar{G}, -\sigma, \Psi_A(T), a}(x)_v = \Psi_V(F_{\bar{G}, -\sigma, \Psi_A(T), a}(x))_v,
\]

for each \(x \notin \Delta_T\). Taking into account lemma 1, \(F_{\bar{G}, -\sigma, \Psi_A(T), a}(\Psi_V(x)) = \Psi_V(F_{\bar{G}, -\sigma, \Psi_A(T), a}(x))\) for all \(t \in \mathbb{N}\), for almost all \((x, T) \in [0, 1]^4 \times [0, 1]^V\). Since \(\Phi_V\) is an isometry, we immediately have

\[
\text{vol}((T, x) \in [0, 1]^4 \times [0, 1]^4 : P(F_{\bar{G}, -\sigma, \Psi_A(T), a}(\Psi_V(x)) = P(F_{\bar{G}, -\sigma, \Psi_A(T), a}(x))) = 1,
\]

for all \(G := (V, A) \in \mathcal{G}\) with no odd cycles, and every \(\sigma \in \{-1, 1\}^4\). Since both \(\Psi_A\) and \(\Psi_V\) preserve the respective Lebesgue measure, and \(\mathbb{P}_G(G\) admits an odd cycle) = 0, we obtain

\[
\mathbb{P}_{a, \eta}(P = \tau) = \sum_{G \in \mathcal{G}} \mathbb{P}_G(G) \sum_{\sigma \in \{-1, 1\}^4} \mathbb{P}_{A, 1 - \eta}(\sigma)
\]

\[
\times \text{vol}(\{(T, x) : P(F_{\bar{G}, -\sigma, \Psi_A(T), a}(\Psi_V(x)) = \tau\})
\]

\[
= \sum_{G \in \mathcal{G}} \mathbb{P}_G(G) \sum_{\sigma \in \{-1, 1\}^4} \mathbb{P}_{A, 1 - \eta}(\sigma) \text{vol}(\{(T, x) : P(F_{\bar{G}, -\sigma, \Psi_A(T), a}(x) = \tau\})
\]

\[
= \mathbb{P}_{a, 1 - \eta}(P = \tau),
\]

for all \(\tau \in \mathbb{N}\), and this concludes the proof of the first claim in the proposition.

For the second claim, if \(F_{\bar{G}, -\sigma, \Psi_A(T), a}(x) \notin \Delta_T\), then

\[
H(\sigma(u, v)(F_{\bar{G}, -\sigma, \Psi_A(T), a}(x)_u - T(u, v))) = H(-\sigma(u, v)(\Psi_V(F_{\bar{G}, -\sigma, \Psi_A(T), a}(x))_u - \Psi_A(T)(u, v))))
\]

\[
= H(-\sigma(u, v)(F_{\bar{G}, -\sigma, \Psi_A(T), a}(\Psi_V(x))_u - \Psi_A(T)(u, v)))).
\]

Therefore, by lemma 1,

\[
\text{vol}(\{(T, x) \in [0, 1]^4 \times [0, 1]^4 : G_{osc}(F_{\bar{G}, -\sigma, \Psi_A(T), a}, \Psi_V(x)) = G_{osc}(F_{\bar{G}, -\sigma, \Psi_A(T), a}, x)) = 1,
\]

for all \(G := (V, A) \in \mathcal{G}\) all of whose cycles have even length, and every \(\sigma \in \{-1, 1\}^4\). From here, taking into account that \(\mathbb{P}_G(G\) admits an odd cycle) = 0, and the fact that that \(\Psi_A\) and
preserve the Lebesgue measure, we obtain
\[
P_{a, \eta} (G_{osc} = \tilde{G}) = \sum_{G \in \mathcal{G} \subseteq V} P_G \sum_{\sigma \in \{-1, 1\}^4} P_{A, 1-\eta} (-\sigma) \times \text{vol} \{(T, x) : G_{osc}(F_G, -\sigma, \Psi_\eta(T), \Psi_V (x)) = \tilde{G}\} = \sum_{G \in \mathcal{G} \subseteq V} P_G \sum_{\sigma \in \{-1, 1\}^4} P_{A, 1-\eta} (-\sigma) \text{vol} \{(T, x) : G_{osc}(F_G, -\sigma, T, a, x) = \tilde{G}\}
\]
for all \( \tilde{G} \in \mathcal{G} \subseteq V \), and the proof is completed.

\[\Box\]

4. Examples

In this section we present, as a matter of illustration, two families of random digraphs which we have explored numerically. A detailed numerical study, which requires massive calculations, is beyond the scope of this work and is left for future research. Instead, in this section we make some general observations suggested by a preliminary numerical exploration of these examples.

4.1. Two families of random digraphs

We consider two kinds of distributions \( P_G \) on the set \( \mathcal{G} := \{(V, A) : A \subset V \times V\} \) of all directed graphs with vertex set \( V \). On one hand we have a directed version of the classical Erdös–Rényi ensemble, which we define as follows.

Fix a vertex set \( V \) and \( p \in (0, 1) \) and consider the probability distribution \( P_p : \mathcal{G} \rightarrow [0, 1] \) such that

\[
P_p(A) = p^{|A|}.
\]

According to this, a directed graph contains the arrow \((u, v)\) with probability \( p \), and the inclusion of different vertices is independent and identically distributed random variables. The typical Erdös–Rényi graph is statistically homogeneous, and thus suited for mean field treatment. Most of the rigorous results concerning random graphs refer to these kinds of models (see [4, 8] and references therein).

The other family of random digraphs we will refer to derives from the famous Barabási–Albert model of scale-free random graphs, whose popularity relies on the ubiquity of the scale-free property [2, 15]. A dynamical construction of scale-free graphs was proposed by Barabási and Albert in [1] (see [8] for a more rigorous presentation). Their model incorporates two key ingredients: continuous growth and preferential attachment. We implemented their construction as follows. For \( n = 0 \), we take \( G_0 = K_{m_0} \), the complete simple undirected graph in \( m_0 \) vertices. Then, for each \( n \geq 1 \), a new vertex \( v_{n+1} \) is added to the graph \( G_n = (E_n, V_n) \). This new vertex forms new edges with randomly chosen vertices in \( V_n \). The probability for \( v \in V_n \) to be chosen is proportional to its degree in \( G_n \), i.e.

\[
\{v_{n+1}, v\} \in E_{n+1} \text{ with probability } p_n(v) := \frac{\# \{u \in V_n : \{u, v\} \in E_n\}}{\# E_n}.
\]

At the \( (n+1) \)th step we obtain a graph \( G_{n+1} \) with an increased vertex set \( V_{n+1} := V_n \cup \{v_{n+1}\} \) and an enlarged edge set \( E_{n+1} \). This random iteration continues until a predetermined number \( N \) of vertices is obtained. In this scheme we are able to add more than one edge at each iteration. If on the contrary, we allow only one new edge at each time step, and we start with \( m_0 = 2 \) vertices choosing at the 1th step one of the two preexisting vertices to form a new edge with probability 1/2, then the resulting graph would be a random scale-free tree [8]. In any
case, the final graph $G_{N-m_0}$ is turned into a directed graph $G = (V, A)$ by randomly assigning a direction to each edge $\{u, v\} \in E_{N-m_0}$. In our case we choose one of the two possible directions with probability $1/4$, and give probability $1/2$ to the choice of both directions. This procedure generates a probability distribution $P_{BA}$ in $G_V := \{(V, A) : A \subset V \times V\}$.

4.2. Erdo\-s–R\-enyi

We generated random digraphs of the Erdo\-s–R\-enyi kind with 100 vertices, and probability of connection $p \in \{0.2, 0.4, 0.6, 0.8\}$. For $p$ fixed and each $\eta \in \{0, 0.1, 0.2, \ldots, 1\}$, we build 20 graphs, to which we randomly and uniformly assign thresholds and signs with probability $P_{A,\eta}$. By taking $a \in \{0.0, 0.1, 0.2, \ldots, 0.8\}$, we obtain 7920 regulatory networks, 20 for each triplet $(p, a, \eta) \in \{0.2, 0.4, 0.6, 0.8\} \times \{0.0, 0.1, 0.2, \ldots, 1\} \times \{0, 0.1, 0.2, \ldots, 1\}$. Finally, for each one of those dynamical systems we run 30 initial conditions randomly taken from $[0, 1]^{100}$, and we let the system evolve in order to determine the corresponding oscillatory subnetwork and the asymptotic period.

The characteristics of the oscillatory subnetwork depend strongly on the parameter $a$ and less noticeably on $\eta$. We have observed that the mean size of the oscillatory subnetwork decreases with $a$ in a seemingly monotonic way and does not appear to depend on $\eta$. The mean number of connected components never exceeded 2. A crude inspection of the degree distributions of the oscillatory subnetworks suggests that they form an ensemble of the Erdo\-s–R\-enyi type; nevertheless, any conclusion in this direction requires a more detailed numerical study. Finally, the mean value of the asymptotic period seems to grow with both $a$ and $\eta$. It increases monotonically with $a$, while for each fixed $a$, it reaches a local maximum around $\eta = 0.5$.

As a matter of illustration, in figure 1 we show two digraphs with vertex set $V = \{1, 2, \ldots, 50\}$. At the left side we draw a random digraph $G \in G_V$ according to the distribution $P_p$, with $p = 0.1$. The signs of the arrows correspond to a random choice according to $P_{A,0.5}$, with $\eta = 0.5$, i.e. both signs have the same probability of being chosen. The digraph at the right is the oscillatory subnetwork $\tilde{G} = G_{osc}(F_{G,a,T,a}, \mathbf{x})$, corresponding to a certain choice of thresholds $T \in [0, 1]^4$ and initial condition $\mathbf{x} \in [0, 1]^V$. The contraction...
Figure 2. A Barabási–Albert network and corresponding oscillatory subnetwork. The underlying graph was built according to the procedure described in section 4.1, starting with \( m_0 = 3 \) vertices. The oscillatory subnetwork corresponds to a random initial condition, with random threshold values, and contraction rate \( a = 0.2 \). In the online version of this paper signs appear codified by colours: blue for +1, and red for −1. They appear with equal probability \( \eta = 0.5 \). In the oscillatory subnetwork, the direction of the arrows is indicated by marking the head with a × sign.

rate was \( a = 0.2 \). In the oscillatory subnetwork, the direction of an arrow \((u, v)\) is indicated by marking head \( v \) with a × sign.

4.3. Barabási–Albert

Following the procedure described in section 4.1 we generate, starting from a complete graph in \( m_0 = 5 \) vertices, ensembles of random digraphs of the Barabási–Albert kind of size \( N = 100 \). For each \( \eta \in \{0, 0.1, 0.2, \ldots, 1\} \), we generate 20 random graphs, then we turn them into directed graphs by choosing one of the two possible directions with probability \( 1/4 \), and both directions with probability \( 1/2 \). Finally, we randomly assign thresholds, and signs with probability \( P_{A,\eta} \), to each one of the 20 resulting digraphs. By ranging \( a \in \{0.0, 0.2, 0.4, 0.6\} \), we obtain 880 regulatory networks, 20 for each couple \((a, \eta)\) \( \in \{0.0, 0.2, 0.4, 0.6\} \times \{0, 0.1, 0.2, \ldots, 1\} \). Then, for each one of those dynamical systems, we randomly select 30 initial conditions in \([0, 1]^{100}\), and let the system evolve in order to determine the corresponding oscillatory subnetwork and the asymptotic period.

For this family of random networks, the mean size of the oscillatory subnetwork behaves in a similar way as for the Erdős–Rényi family, i.e. it increases nonmonotonically with \( \eta \), with a local maximum at \( \eta = 0.5 \), and decreases monotonically with \( a \). The mean number of connected components (ranging from 0 to 10) shows a similar behaviour with respect to both \( \eta \) and \( a \), with a very noticeable increase around \( \eta = 0.5 \). On the other hand, the distribution of the asymptotic period becomes broader as we approach \( \eta = 0.5 \), and for each value of \( \eta \), the mean value of the asymptotic period grows with \( a \). It is worth noting that these distributions become broader as \( a \) increases, and at the same time the number of connected components grows. This behaviour is consistent with the proliferation of periods predicted by corollary 1, in the case of a statistical ensemble whose oscillatory subnetworks have many connected components.

In figure 2 we show two digraphs with vertex set \( V = \{1, 2, \ldots, 50\} \). At the left side we draw a random digraph \( G \in \mathcal{G}_V \) according to the distribution \( P_{BA} \). The sign of the arrows is randomly chosen by using the distribution \( P_{A,\eta} \) with \( \eta = 0.5 \), i.e. both signs have the same probability. The digraph at the right is the oscillatory subnetwork \( G = G_{osc}(F_{G,a,T,u},x) \), determined by a random choice of thresholds \( T \in [0, 1]^4 \) and initial condition \( x \in [0, 1]^V \), with
contraction rate $a = 0.2$. In the oscillatory subnetwork, the direction of the arrows is indicated by marking the head with a $\times$.

In figure 3 we show the behaviour of the probability of approaching a fixed point, and the probability of an asymptotic period of length 2, both as a function of $a$ and $\eta$. This picture summarizes the statistics of the 26400 orbits generated on Barabási–Albert like networks and presents the symmetry $\eta \rightarrow 1 - \eta$ predicted by proposition 1. This symmetry is expected in an ensemble of regulatory networks whose underlying digraphs have no odd length cycles. Though the underlying networks of the experiments we performed have both odd and even length cycles, there is a larger proportion of even lengths amongst the cycles of small length.

5. Proofs

5.1. Proof of theorem 1

Given $\mathcal{G} = (V, A)$, we will use the distance $d_{\text{max}}(x, y) := \max_{i} |x_i - y_i|$ in both $[0, 1]^V$ and $[0, 1]^A$. As usual, $d_{\text{max}}(x, E) := \inf \{d_{\text{max}}(x, y) : y \in E\}$ for $x \in [0, 1]^F$ and $E \subset [0, 1]^F$.

First notice that for $\mathcal{G}$, $\sigma$ and $a$ fixed, the set

$$O_{\mathcal{G}, \sigma, a} := \{(T, x) \in [0, 1]^A \times [0, 1]^V : \inf_{t \geq 0} d_{\text{max}}(F_{\mathcal{G}, \sigma, T, a}^t (x), \Delta_T) > 0\}$$

(10)

is open. Indeed, if $(T, x) \in O_{\mathcal{G}, \sigma, a}$, then $d_{\text{max}}(F_{\mathcal{G}, \sigma, T, a}^t (x), \Delta_T) > 3\varepsilon$, for some $\varepsilon > 0$ and all $t \geq 0$. The orbit does not change if we perturb $T$, i.e. for each $T' \in B_{\varepsilon}(T)$ we have...
such that $550 A Cros$

5.1.1. The asymptotic period is measurable in $O_{\sigma,a}$

that for each $G$, $\sigma$ and $a$ fixed, the set $O_{\sigma,a}$ is open in $[0,1]^4 \times [0,1]^V$, then

$$O_{\sigma,a,V} := \bigcup_{\theta} \bigcup_{\sigma \in \{-1,1\}^4} \bigcup \{(F_{G,\sigma,a}, x) : (T, x) \in O_{G,a}\}$$

is measurable in $\mathcal{F}_{\sigma,a} \times [0,1]^V$.

5.1.1. The asymptotic period is measurable in $O_{\sigma,a}$

Fix $G$, $\sigma$ and $a$, and take $(T, x) \in O_{G,\sigma,a}$ such that $P(F_{G,\sigma,a}, x) = \tau$. There exists $\tilde{y} \in \text{Per}_\tau(F_{G,\sigma,a})$ and $N \in \mathbb{N}$, such that

$$d_{\max}(F_{G,\sigma,a}^N(x), \tilde{y}) < \varepsilon := \frac{\inf_{i \geq 0} d_{\max}(F_{G,\sigma,a}^i(x), \Delta_T)}{3}.$$ 

Hence, for each $t \geq 0$ we have $d_{\max}(F_{G,\sigma,a}^{N+t}(x), F_{G,\sigma,a}^t(L_t \tau)) < a \varepsilon$. By the same argument as in the previous paragraph, $d_{\max}(F_{G,\sigma,a}^{N+t}(x), F_{G,\sigma,a}^t(L_t \tau)) < a \varepsilon + a N \varepsilon < 2a \varepsilon$ for all $t \geq 0$.

Therefore $P(F_{G,\sigma,a}, y) = \tau$ for all $(T', y) \in B_{\varepsilon}(T) \times B_{\varepsilon}(x)$. In this way we have proved that for each $G$, $\sigma$ and $a$ fixed, the set

$$O_{G,\sigma,a}^{\{1\}} := \{(T, x) \in [0,1]^4 \times [0,1]^V : P(F_{G,\sigma,a}, x) = \tau\}$$

is an open set in $[0,1]^4 \times [0,1]^V$, therefore

$$P^{-1}\{1\} \cap O_{\sigma,a,V} := \bigcup_{\theta} \bigcup_{\sigma \in \{-1,1\}^4} \bigcup \{(F_{G,\sigma,a}, x) : (T, x) \in O_{G,\sigma,a}^{\{1\}},\}$$

is measurable in $\mathcal{F}_{\sigma,a} \times [0,1]^V$.

5.1.2. The asymptotic period is finite in $O_{\sigma,a}$

For $(F_{G,\sigma,a}, x) \in O_{\sigma,a}$ let $\hat{x} \in \text{closure}(\{F_{G,\sigma,a}^t(x) : t \in \mathbb{N}\})$ be such that

$$\inf_{t \geq 0} d_{\max}(F_{G,\sigma,a}^t(x), \Delta_T) = d_{\max}(\hat{x}, \Delta_T) = \varepsilon > 0.$$ 

Notice that $(F_{G,\sigma,a}, \hat{x}) \in O_{\sigma,a}$ too, and $\inf_{t \geq 0} d_{\max}(F_{G,\sigma,a}^t(\hat{x}), \Delta_T) = d_{\max}(\hat{x}, \Delta_T) = \varepsilon$.

For $N \in \mathbb{N}$ such that $d_{\max}(F_{G,\sigma,a}^N(x), \hat{x}) < \varepsilon$ we have $d_{\max}(F_{G,\sigma,a}^N(x), F^t(\hat{x})) < a \varepsilon$ for all $t \geq 0$. Now, for $r \in \mathbb{N}$ such that $a^r < 1/4$ and $d_{\max}(F_{G,\sigma,a}^N(x), \hat{x}) < \varepsilon/4$, we have

$$d_{\max}(F_{G,\sigma,a}^N(\hat{x}), \hat{x}) < d_{\max}(F_{G,\sigma,a}^{N+t}(x), \hat{x}) + d_{\max}(F_{G,\sigma,a}^N(x), \hat{x}) < \varepsilon/4 + a^r \varepsilon < \varepsilon/2.$$ 

Since $\inf_{t \geq 0} d_{\max}(F_{G,\sigma,a}^t(\hat{x}), \Delta_T) = \varepsilon$, then

$$d_{\max}(F_{G,\sigma,a}^{N+t}(\hat{x}), \hat{x}) < \frac{\varepsilon}{2^{2k-1}}$$

for all $k \in \mathbb{N}$. Hence $\hat{y} := \lim_{k \to \infty} F_{G,\sigma,a}^{N+k}(\hat{x})$ exists and satisfies $F_{G,\sigma,a}^N(\hat{x}) = \hat{y}$. Furthermore, since $d_{\max}(\hat{x}, \hat{y}) < \varepsilon$, for all $s \in \mathbb{N}$, we have

$$d_{\max}(F_{G,\sigma,a}^{N+k}(\hat{x}), \hat{y}) < d_{\max}(F_{G,\sigma,a}^{N+k}(\hat{x}), F_{G,\sigma,a}^N(\hat{x}), \hat{y}) + d_{\max}(F_{G,\sigma,a}^N(\hat{x}), \hat{y}) < \frac{5a^{k} \varepsilon}{3},$$

for each $k \in \mathbb{N}$, which implies $\lim_{k \to \infty} F_{G,\sigma,a}^{N+k}(\hat{x}) = \hat{y}$. It follows from here that $P(F_{G,\sigma,a}, x) = \tau$. In addition, since $\hat{y} \in \text{closure}(\{F_{G,\sigma,a}^t(x) : t \in \mathbb{N}\})$, then $\min_{0 \leq t < \tau} d_{\max}(F_{G,\sigma,a}^t(\hat{y}), \Delta_T) = \varepsilon$. 

5.1.3. The complement of $O_{\sigma,V}$ has zero measure for $a < \max_{v \in V} (\operatorname{Id}(u) + 1)^{-1}$. Fix $G, \sigma, a$, and for $(T, x) \notin O_{\sigma,a}$ let $D^{(n)} := D_{G,\sigma,a}(F_{G,\sigma,T,a}^n(x))$ for each $n \in \mathbb{N}$. Then, there exists a sequence $\{t_k\}_{k \in \mathbb{N}}$, and $u, v \in V$, such that

$$T_{(u,v)} = \lim_{k \to \infty} \left( a^k x_u + (1 - a) \sum_{t=1}^{t_k} a^{t-1} D_u^{(t_k-t)} \right)$$

$$= (1 - a) \lim_{k \to \infty} \left( \sum_{t=1}^{t_k} a^{t-1} D_u^{(t_k-t)} \right).$$

(12)

For each $x \in [0, 1]^V$ fixed, define the fibre

$$C_{G,\sigma,a}(x) := \{ T \in [0, 1]^A : (T, x) \notin O_{G,\sigma,a} \}.$$

(13)

Then, according to equation (12) we have

$$C_{G,\sigma,a}(x) \subset \bigcup_{(u,v) \in A} \left\{ T \in [0, 1]^A : T_{(u,v)} \in \frac{1 - a}{\operatorname{Id}(u)} \times \text{closure}(\Omega_{G,a,u}) \right\},$$

where

$$\Omega_{G,a,u} := \bigcup_{N=1}^{\infty} \left\{ \sum_{s=0}^{N-1} a^s k_s : (k_s)_{s=0}^{N-1} \in \{0, 1, \ldots, \operatorname{Id}(u)\}^N \right\}.$$

If $a < (\operatorname{Id}(u) + 1)^{-1}$ for some $u \in V$, then $\text{closure}(\Omega_{G,a,u})$ is a Cantor set of dimension $\log(\operatorname{Id}(u)+1)/\log(1/a) < 1$. Hence, Fubini’s theorem implies, for $a < \max_{v \in V} (\operatorname{Id}(u) + 1)^{-1}$, that the fibre $C_{G,\sigma,a}(x)$ has zero $A$-dimensional volume for each $x \in [0, 1]^V$.

5.1.4. The complement of $O_{\sigma,V}$ has zero measure for $a \geq \max_{v \in V} (\operatorname{Id}(u) + 1)^{-1}$. The fact that $\text{vol}(C_{G,\sigma,a}(x)) = 0$ for each $x \in [0, 1]^A$ and arbitrary $a \in (0, 1)$ derives from a result by Kruglikov and Rypdal. Theorem 2 in [12] gives an upper bound for the topological entropy of the symbolic system associated with a nondegenerated piecewise affine map. The upper bound is related to the exponential rate of angular expansion under the action of the map. For piecewise affine conformal maps, which is the case of discrete-time regulatory networks, this upper bound vanishes. Hence, Kruglikov and Rypdal’s theorem directly applies to our case, implying that

$$\lim_{N \to \infty} \frac{\log \# \mathcal{L}^{(N)}_{(T,x,u)}}{N} = 0,$$

(14)

where for each $G, \sigma$ and $a$ fixed,

$$\mathcal{L}^{(N)}_{(T,x,u)} := \{ (k_{t+1})_{t=0}^{N-1} \in \{0, 1, \ldots, \operatorname{Id}(u)\}^N : D_{G,\sigma,T}(F_{G,\sigma,T,a}^n(x))_a = \frac{k_t}{\operatorname{Id}(u)} \forall t \in \mathbb{N} \}.$$

Therefore, for each $T$, there exists $N = N(T,x,u) \in \mathbb{N}$ such that $\# \mathcal{L}^{(N)}_{(T,x,u)} \leq ((1 + a)/2a)^N$. Fix $u \in V$, and for each $N \in \mathbb{N}$ and $D \subset \{0, 1, \ldots, \operatorname{Id}(u)\}^N$, define

$$T_D := \left\{ x = \sum_{t=0}^{\infty} a^t k_t : (k_{t+1})_{t=0}^{N-1}, \ldots, k_{kN} \in D \forall k \geq 0 \right\}.$$

With this we have, for the fibre $C_{G,\sigma,a}(x)$ defined in (13), the inclusion

$$C_{G,\sigma,a}(x) \subset \bigcup_{(u,v) \in A} \bigcup_{N \in \mathbb{N}} \bigcup_{\mathcal{L}^{(N)}_{(T,x,u)} \leq ((1 + a)/2a)^N} \left\{ T \in [0, 1]^A : T_{(u,v)} \in \frac{1 - a}{\operatorname{Id}(u)} \times \text{closure}(T_D) \right\}.$$
Now, for each \( m \in \mathbb{N} \), a prefix \( k \in (L(N)(T,x,u))^m \) defines an interval
\[
I_k := \left\{ x = \sum_{t=0}^{\infty} \omega_t a^t : (\omega_t)_{t=0}^{mN-1} = (k_{mN-t})_{t=1}^{mN} \right\},
\]
and we have
\[
\text{closure}(T_D) = \bigcap_{m=1}^{\infty} \left( \bigcup_{k \in D^m} \text{closure}(I_k) \right).
\]
Since \( \text{vol}(I_k) = \text{vol}(\text{closure}(I_k)) = \frac{\text{Id}(u)mN}{1-a} \) for each \( k \in (L(N)(T,x,u))^m \), then
\[
\text{vol}(\text{closure}(T_D)) \leq \frac{\#D}{1-a} \frac{\text{Id}(u)mN}{1-a},
\]
for each \( m \in \mathbb{N} \). Hence, \( \text{vol}(\text{closure}(T_D)) = 0 \) for each \( D \subset \{0,1,\ldots,\text{Id}(u)\}^N \) such that \( \#D \leq ((1+a)/2a)^N \). Taking into account (15), Fubini’s theorem implies, that the fibre \( C_{\tilde{G},\sigma,a}(x) \) has zero \#A-dimensional volume for each \( x \in [0,1]^V \).

Using once again Fubini’s theorem, we finally conclude that
\[
\mathbb{P}_{a,\eta}(F_{a,V} \times [0,1]^V \setminus O_{a,V}) \leq \sum_{\hat{G} \in \mathcal{G}_V} \sum_{\sigma \in \{-1,1\}^A} \mathbb{P}_{\hat{G},\eta} \mathbb{P}_{A,\eta} \int_{x \in [0,1]^V} \text{vol}(C_{\tilde{G},\sigma,a}(x)) \, dx = 0.
\]

**Remark 1.** In the statement of theorem 1 we can replace the probability measure \( \mathbb{P}_{a,\eta} \) by any other Borel measure \( \mathbb{P} \) in \( F_{a,V} \times [0,1]^V \) such that, for each \( \hat{G} \in \mathcal{G}_V, \sigma \in \{-1,1\}^A \), and \( x \in [0,1]^V \) fixed, the \#A-dimensional projection
\[
\mathbb{P}_{\hat{T}}(J) := \mathbb{P}\{ (F_{G,\sigma,T,a},x) \in F_{a,V} \times [0,1]^V : T \in J \}
\]
is absolutely continuous with respect to the Lebesgue measure.

**Remark 2.** From the arguments developed in section 5.1.3, it follows that for \( a < \min_{u \in V} (\text{Id}(u) + 1)^{-1} \), the set \( O_{G,\sigma,a} \) defined in (10) is open and dense. This ensures that orbits are generically uniformly far from the discontinuity set. As a consequence, periodic attractors not intersecting the discontinuity set are generic for \( a < \min_{u \in V} (\text{Id}(u) + 1)^{-1} \). On the other hand, the argument in section 5.1.4 ensures, as long as we consider distributions absolutely continuous with respect to Lebesgue for thresholds, that orbits are almost certainly uniformly far from the discontinuity set. Hence, in the general case, almost all initial conditions converge to periodic attractors not intersecting the discontinuity set.

### 5.2. Proof of theorem 2

This theorem consists of two claims. The first one establishes the stability of the oscillatory subnetworks, while the second one gives the equivalence between the dynamics restricted to that subnetwork and the dynamics supported by the subnetwork considered as an isolated system. Both claims follow from direct computations.
5.2.1. Stability of the oscillatory subnetworks. Since \( P_{\sigma,t}(G_{\text{osc}} = \tilde{G}) > 0 \), there exists \( \tilde{G} \in \mathcal{F}_{\nu} \), \( \sigma \in [-1, 1]^A \), and \( (\tilde{T}, \tilde{x}) \) such that \( G_{\text{osc}}(G_{\tilde{G}, \sigma, \tilde{T}, \mu, \tilde{x}}) = \tilde{G} \). As proved in section 5.1.2, there exists 0 < \( \varepsilon < 1/2 \), \( \tau \in \mathbb{N} \), and \( \tilde{y} \in \text{Per}_r(G_{\tilde{G}, \sigma, \tilde{T}, \mu}) \), such that

\[
\lim_{t \to \infty} |F_{\tilde{G}, \sigma, \tilde{T}, \mu, \tilde{x}}(\tilde{x}) - F_{\tilde{G}, \sigma, \tilde{T}, \mu, \tilde{x}}(\tilde{y})| = 0
\]

and

\[
\inf_{t \geq 0} d_{\text{max}}(F_{\tilde{G}, \sigma, \tilde{T}, \mu, \tilde{x}}(\tilde{x}), \Delta_T) = \min_{\tilde{y} \in \mathcal{T}} d_{\text{max}}(F_{\tilde{G}, \sigma, \tilde{T}, \mu, \tilde{x}}(\tilde{y}), \Delta_T) = 2\varepsilon.
\]

From this it readily follows that \( G_{\text{osc}}(G_{\tilde{G}, \sigma, \tilde{T}, \mu, \tilde{x}}) = \tilde{G} \) for each \( (\tilde{T}, \tilde{x}) \in B_{\tau}(\tilde{T}) \times B_{\tau}(\tilde{x}) \).

Let us now extend \( G, \sigma \) and \( \tilde{T} \), and redefine \( \tilde{y} \) at each vertex \( v \in \tilde{V} \) such that \( \text{Id}_{\text{osc}}(v) = \text{Id}(v) \) (remind that \( \text{Id}_{\text{osc}}(v) : = \#\{u \in V : (u, v) \in A \equiv A_{\text{osc}}\} \)). Choose \( u \notin \tilde{V} \), and include the arrow \((u, v) \in A\). Then, if \( \tilde{y}_u < 1 - 2\varepsilon \), define \( \sigma_{(u, v)} = 1 \) and \( \tilde{T}_{(u, v)} = 1 - \varepsilon \). Otherwise, if \( \tilde{y}_u > 2\varepsilon \), make \( \sigma_{(u, v)} = -1 \) and \( \tilde{T}_{(u, v)} = \varepsilon \). Finally, redefine \( \tilde{y}_v = \text{Id}(v) \tilde{y}_v / (\text{Id}(v) + 1) + 1/(\text{Id}(v) + 1) \) at that vertex. A simple computation shows that, in the redefined system, \( G_{\text{osc}}(G_{\tilde{G}, \sigma, \tilde{T}, \mu, \tilde{x}}) = \tilde{G} \), for each \( (\tilde{T}, \tilde{x}) \in B_{\tau}(\tilde{T}) \times B_{\tau}(\tilde{x}) \). Therefore, taking into account that by hypothesis \( P_0(G) > 0 \) for all \( G \in \mathcal{F}_{\nu} \), we can assume without loss of generality that \( \text{Id}_{\text{osc}}(v) < \text{Id}(v) \) for all \( v \in \tilde{V} \).

By definition, if \((u, v) \in A \setminus \tilde{A}\) then \( \theta_{(u, v)} := H(\sigma_{(u, v)}(\tilde{y}_v - \tilde{T}_{(u, v)}) \) remains constant in time, as well as \( D(v) := \sum_{(x,v) \in A \setminus \tilde{A}} \theta_{(x, v)} \) for each \( v \in \tilde{V} \). Let us now modify \( \sigma \) and \( \tilde{T} \) for the arrows leaving \( \tilde{G} \). For \( u \in \tilde{V} \), and each \( v \notin \tilde{V} \), if \( D(u) > 0 \), make \( \tilde{T}_{(u, v)} \rightarrow \tilde{T}_{(u, v)} \times D(u)/\text{Id}(u) \), and

\[
\sigma_{(u, v)} \mapsto \begin{cases} 
\sigma_{(u, v)} + \sigma_{(u, v)} & \text{if } \theta_{(u, v)} \in [-1, 2], \\
-\sigma_{(u, v)} & \text{if } \theta_{(u, v)} + \sigma_{(u, v)} \in [0, 1].
\end{cases}
\]

Otherwise, if \( D(u) = 0 \), then \( \tilde{T}_{(u, v)} \rightarrow \tilde{T}_{(u, v)} \times (\text{Id}(u) - \text{Id}_{\text{osc}}(u))/\text{Id}(u) + \text{Id}_{\text{osc}}(u))/\text{Id}(u) \), and

\[
\sigma_{(u, v)} \mapsto \begin{cases} 
-\sigma_{(u, v)} & \text{if } \theta_{(u, v)} + \sigma_{(u, v)} \in [-1, 2], \\
\sigma_{(u, v)} & \text{if } \theta_{(u, v)} + \sigma_{(u, v)} \in [0, 1].
\end{cases}
\]

This modification in \( \sigma \) and \( \tilde{T} \) uncouples the dynamics on \( \tilde{V} \) from that on \( V \setminus \tilde{V} \), so that now we can set \( \tilde{\sigma} \equiv \tilde{\sigma} \) for arbitrary \( \tilde{\sigma} \in [-1, 1]^A \). In this way we obtain a digraph extension \( \tilde{G}_{\text{ext}} := \tilde{G} \supset \tilde{G} \), and for each \( \tilde{\sigma} \in [-1, 1]^A \), an extension \( \tilde{G}_{\text{ext}} := \sigma \in [-1, 1]^A \) with \( \tilde{G}_{\text{ext}} \equiv \tilde{\sigma} \). For any of these extensions, a direct computation shows that \( \lim_{t \to \infty} F_{\tilde{G}_{\text{ext}}, \tilde{\sigma}, \tilde{T}, \mu}(x)_v = D(v)/\text{Id}(v) \), for \( v \notin \tilde{V} \), and \( F_{\tilde{G}_{\text{ext}}, \tilde{\sigma}, \tilde{T}, \mu}(x)_v \in [D(v)/\text{Id}(v), (D(v) + \text{Id}_{\text{osc}}(v))/\text{Id}(v)] \), for all \( t \geq 0 \) and \( v \in \tilde{V} \), whenever

\[
x \in \tilde{J} \times \mathcal{J}' := \left( \prod_{v \notin \tilde{V}} B_{\varepsilon} (\tilde{y}_v - \varepsilon, \tilde{y}_v + \varepsilon] \cap [0, 1] \right) \times \left( \prod_{v \in \tilde{V}} \frac{[D(v)/\text{Id}(v), (D(v) + \text{Id}_{\text{osc}}(v))/\text{Id}(v)]}{[D(v)/\text{Id}(v), (D(v) + \text{Id}_{\text{osc}}(v))/\text{Id}(v)]} \right)
\]

and

\[
T \in \tilde{I} \times \mathcal{I}' := \left( \prod_{(u, v) \in A \setminus \tilde{A}} \tilde{T}_{(u, v)} - \varepsilon, \tilde{T}_{(u, v)} + \varepsilon] \cap [0, 1] \right) \times \left( \prod_{(u, v) \in A \setminus \tilde{A}} \frac{[D(u)/\text{Id}(u), (D(u) + \text{Id}_{\text{osc}}(u))/\text{Id}(u)]}{[D(u)/\text{Id}(u), (D(u) + \text{Id}_{\text{osc}}(u))/\text{Id}(u)]} \right).
\]

Therefore, \( G_{\text{osc}}(F_{\tilde{G}_{\text{ext}}, \tilde{\sigma}, \tilde{T}, \mu, \tilde{x}}) \subseteq \tilde{G} \) for each \( (T, x) \in I \times \mathcal{J} := (\tilde{I} \times \mathcal{I}) \times (\tilde{J} \times \mathcal{J}') \), and \( \tilde{\sigma} \in [-1, 1]^A \).
5.2.2. Equivalence to the subnetwork considered as an isolated system. We will use the same notation as in subsection 5.2.1. Let $\sigma := \sigma_{\text{ext}}$, and each $(T, x) \in (I \times I') \times (J \times J')$, and $t \in \mathbb{N}$, let $x' := F_{\sigma, \text{ext}, T, a}(x)$. For each $v \in V$, the term

$$D(v) := \sum_{(u,v) \in A \setminus \tilde{A}} H(\sigma_{(u,v)}(x'_u - T_{(u,v)})) = \sum_{(u,v) \in A \setminus \tilde{A}} H(\sigma_{(u,v)}(F'_{G, \sigma, T, a}(y)_u - \tilde{T}_{(u,v)}))$$

remains constant in time. Since $\sigma|_{\tilde{A}} \equiv \tilde{\sigma}$,

$$x^{t+1}_v = ax'_v + \frac{\text{Id}_{\text{osc}}(v)}{\text{Id}(v)} \left( \frac{1 - a}{\text{Id}_{\text{osc}}(v)} \sum_{(u,v) \in \tilde{A}} H(\tilde{\sigma}_{(u,v)}(x'_u - T_{(u,v)})) \right) + (1 - a) \frac{D(v)}{\text{Id}(v)},$$

which can be rewritten as

$$\Phi_V(x^{t+1})_v = a\Phi_V(x'_v) + \frac{1 - a}{\text{Id}_{\text{osc}}(v)} \sum_{(u,v) \in \tilde{A}} H(\tilde{\sigma}_{(u,v)}(\Phi_V(x'_u) - \Phi_{\tilde{A}}(T_{(u,v)}))),$$

(16)

where $\Phi_{\tilde{A}} : \tilde{I} \times I' \to [0, 1]^{\tilde{A}}$ and $\Phi_V : \tilde{J} \times J' \to [0, 1]^\tilde{V}$ are affine transformations defined as follows. We have $\Phi_{\tilde{A}}(\tilde{I} \times I') = D_{\tilde{A}} \tilde{T} + C_{\tilde{A}}$, with

$$(D_{\tilde{A}} \tilde{T})_{(u,v)} = \frac{\text{Id}(u)}{\text{Id}_{\text{osc}}(u)} \times \tilde{T}_{(u,v)}$$

and

$$(C_{\tilde{A}})_{(u,v)} = -\frac{D(u)}{\text{Id}_{\text{osc}}(u)},$$

for each $(u, v) \in \tilde{A}$, and $\Phi_V(\tilde{x} \times x') = D_{\tilde{V}} \tilde{x} + C_{\tilde{V}}$, with

$$(D_{\tilde{V}} \tilde{x})_v = \frac{\text{Id}(v)}{\text{Id}_{\text{osc}}(v)} \times \tilde{x}_v$$

and

$$(C_{\tilde{V}})_v = -\frac{D(v)}{\text{Id}_{\text{osc}}(v)},$$

for each $v \in \tilde{V}$. The result follows from equation (16), which establishes

$$F_{G, \tilde{A}, \Phi_{\tilde{A}}(T, a)}(\Phi_V(x)) = \Phi_V(F_{G, \text{ext}, \tilde{A}, T, a}(x))$$

for all $(T, x) \in I \times J$, and from the fact that $\Phi_{\tilde{A}}$ and $\Phi_V$ are affine and surjective. □

Remark 3. In the statement of theorem 2, instead of the hypothesis $\mathbb{P}_G(\mathcal{G}) > 0$ for all $\mathcal{G} \in \mathfrak{G}_V$, we could have directly supposed that the oscillatory subnetwork $\tilde{G} := (\tilde{V}, \tilde{A})$ is such that $\text{Id}_{\text{osc}}(v) < \text{Id}(v)$ for each $v \in \tilde{V}$. By assuming this, we avoid the condition $\tilde{V} \subset V$ as well. This alternative formulation allows us to consider the emergence of modularity in Barabási–Albert random networks, for which $\mathbb{P}_{\text{BA}}(\mathcal{G}) = 0$ for some digraphs $\mathcal{G} \in \mathfrak{G}_V$.

6. Final comments and conclusions

From our point of view, one of the most important theoretical problems in regulatory dynamics concerns the relations between the structure of the underlying network and the possible dynamical behaviours the system generates. We have already established bounds relating the structure of the underlying network and the growth of distinguishable orbits [16]. Here, following [22], we have considered regulatory networks with interactions and initial conditions chosen at random at the beginning of the evolution. Within this approach, individual orbits become elements in a sample space, and the characteristics of the asymptotic behaviour can be considered as orbit dependent random variables. The structure of the underlying network, random in this approach, is encoded in a probability distribution over a set of directed graphs. In two interesting cases we have explored, the asymptotic oscillations concentrate on a relatively
small subnetwork, whose structure depends on both the proportion of inhibitory interactions and the contraction rate. We have proved that the dynamics observed on this subnetwork is equivalent to the dynamics supported by the subnetwork considered as an isolated system. We interpret this as the emergence of modularity. Modularity allows us to predict asymptotic periods in regulatory networks admitting disconnected oscillatory subnetworks.

We want to remark theorem 1, which has important technical implications. It ensures, as long as we consider distributions absolutely continuous with respect to Lebesgue for thresholds and initial conditions, that a random orbit converges to a periodic attractor. Furthermore, this periodic attractor does not intersect the discontinuity set. We have also proved, in the case of small contraction rates, that the periodic attractors are generic. This can be deduced from the argument in section 5.1.3.

As mentioned above, in order to determine the distribution of the asymptotic period, and the characteristics of the oscillatory subnetwork, a detailed numerical study of the examples presented in section 4 is required. Heuristic computations could guide those numerical studies, and it is our intention to proceed in this direction in a subsequent work.

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References

[1] Barabási A–L and Albert R 1999 Emergence of scaling in random networks Science 286 509–12
[2] Barabási A–L and Oltvai Z N 2004 Network biology: understanding the cell’s functional organization Nature Rev. Genetics 5 101–13
[3] Bastolla U and Parisi G 1998 The modular structure of Kauffman networks Physica D 115 219–33
[4] Bollobas B 2001 Random graphs Cambridge Studies in Advanced Mathematics vol 73 (Cambridge: Cambridge University Press)
[5] Coutinho R, Fernandez B, Lima R and Meyroneinc A 2006 Discrete–time piecewise affine models of genetic regulatory networks J. Math. Biol. 52 524–70
[6] de Jong H 2002 Modeling and simulation of genetic regulatory systems: a literature review J. Comput. Biol. 969–105
[7] de Jong H and Lima R 2005 Modeling the Dynamics of Genetic Regulatory Networks: Continuous and Discrete Approaches (Lecture Notes in Physics vol 671) pp 307–40
[8] Durrett R 2007 Random Graph Dynamics (Cambridge Series in Statistical and Probabilistic Mathematics vol 20) (Cambridge: Cambridge University Press)
[9] Edwards R 2000 Analysis of continuous-time switching networks Physica D 146 165–99
[10] Gómez–Gardeñes J, Moreno Y and Floria L M 2006 Scale-free topologies and activatory–inhibitory interactions Chaos 16 015114
[11] Kauffman S A 1969 Metabolic stability and epigenesis in randomly constructed genetic nets J. Theor. Biol. 22 437–67
[12] Kruglikov B and Rypdal M 2006 Entropy via multiplicity Discrete Contin. Dyn. Syst.—Ser. A 16 395–410
[13] Glass K and Kauffman S A 1974 The logical analysis of continuous, nonlinear biochemical control networks J. Theor. Biol. 44 167–90
[14] Glass L and Pasternack J S 1978 Prediction of limit cycles in mathematical models of biological oscillations Bull. Math. Biol. 40 27–44
[15] Jeong H, Tomor B, Albert R, Oltvai Z N and Barabási A–L 2000 The large–scale organization of metabolic networks Nature 407 651–4
[16] Lima R and Ugalde E 2006 Dynamical complexity of discrete–time regulatory networks Nonlinearity 19 237–59
[17] Mestl T, Plathe E and Omholt S W 1995 A mathematical framework for describing and analyzing gene regulatory networks J. Theor. Biol. 176 291–300
[18] Naldi A, Thieffry D and Chaouiya C 2007 Decision diagrams for the representation and analysis of logical models of genetic networks Computational Methods in System Biology 2007 (Lecture Notes in Bioinformatics) vol 4695 (Berlin: Springer) pp 233–47
[19] Thieffry D and Thomas R 1995 Dynamical behavior of biological networks Bull. Math. Biol. 57 277–97
[20] Thieffry D 2007 Dynamical roles of biological regulatory circuits Briefings Bioinformatics 8 220–25
[21] Thomas R 1973 Boolean formalization of genetic control circuits J. Theor. Biol. 42 563–85
[22] Volchenkov D and Lima R 2005 Random shuffling of switching parameters in a model of gene expression regulatory network Stoch. Dyn. 5 75–95