Stability and steady state of complex cooperative systems: a diakoptic approach

Philip Greulich[1,2], Benjamin D. MacArthur[1,2], Cristina Parigini[1,2], and Rubén J. Sánchez García[1,2]

[1]School of Mathematical Sciences, University of Southampton, Southampton, UK
[2]Institute for Life Sciences, University of Southampton

July 17, 2019

Abstract

Cooperative dynamics are common in ecology and population dynamics, and are a hallmark of stochastic processes. However, their commonly high degree of complexity with a large number of coupled degrees of freedom renders them difficult to analyse. Here we present a graph-theoretical criterion, via a diakoptic approach ("divide-and-conquer") to determine a cooperative system's stability by decomposing the system's interaction graph into its strongly connected components (SCCs). In particular, we show that a linear cooperative system is Lyapunov stable if the SCCs of the associated dependence graph all have non-positive dominant eigenvalues, and if no SCCs which have dominant eigenvalue zero are connected by a path.

1 Introduction

Cooperative systems are a wide class of dynamical systems which include (multi-species) population dynamics, mutually activating chemical reaction networks, and generalised compartment models, which in essence also encompass all discrete-state Markov processes. A cooperative system is one that is defined via non-negative interactions between its components or, alternatively, transitions between compartments. In mathematical terms, a cooperative system is one whose Jacobian matrix has non-negative off-diagonal elements [1].

Cooperative systems can be highly complex, with a large number of variables and complex interactions, in which case their analysis is a highly challenging endeavour. A paradigm to study complex systems is the *diakoptic* view ("divide-and-conquer") [2]: a large interacting system is decomposed into suitable small subsystems, which are studied isolated, a task which is usually easier to perform. Then, in a synthesis step, the properties of subsystems are combined to find the corresponding features of the whole system.

High-dimensional dynamical systems can be represented by directed graphs in which dependent variables $x_i(t), i \in \mathbb{N}$, are nodes and links denote dependence relations between those variables. The Jacobian matrix $J = [\frac{\partial \dot{x}_i}{\partial x_j}]$ of such a system can be interpreted as an adjacency matrix of an underlying graph representing the mutual dependence of components. This analogy between dynamical systems and graphs suggests that graph-theoretical tools may be exploited to determine the stability features of a system.

While general criteria for a cooperative system's stability are well established [3], the calculations involved for particular high-dimensional systems can be difficult and do not always provide intuitive insight. Finding qualitative measures that specify a system's stability, such as the sign of system parameters or the connective properties of the underlying graph, is a worthwhile quest (see for example [4]). Here, we seek to find qualitative criteria for the stability of complex linear cooperative dynamical systems, based on structural features of the underlying dependence graph, viz. the hierarchical arrangement of its strongly connected components.

Most generalised compartmental models, where a positive quantity can transit between states or positions, are cooperative systems [5]. This encompasses linear population dynamics in which individuals may reproduce and die, and can transit between different 'states' or phenotypes, or mutate between genotypes. A common example is that of epidemic models in which individuals of a population transit between different infection states (e.g. susceptible, infected, recovered, in an SIR model [6]) or cells that can switch between different epigentically inherited phenotypes, or differentiate [7]. In absence of an explicit dependence between compartments, such a system is always cooperative, since the dynamics of a variable $x_i(t)$ in state i is completely determined by the inflow of quantities $x_j(t)$ from other states j, which is always non-negative. In that case the system is also linear.

A simple way of using diakoptics to determine conditions for a linear system's *asymptotical* stability is obtained by partitioning the underlying directed graph of a system into its *strongly connected components* (SCCs). A strongly connected component is a maximal subset of nodes which are mutually reachable by directed paths. Simply speaking, a system is asymptotically stable if all its SCCs, when decoupled from each other, are asymptotically stable [8]. However, this simple statement does not apply to general Lyapunov stability, and in particular not to marginal (neutral) stability: It does not follow that a system is (marginally) stable if all or some of its strongly connected components are. The requirement of marginal stability is yet crucial for many linear systems such as the dynamics of neutrally competing subsets of a populations; these are linear since typically non-linear feedback affects the population as a whole but not small subsets. In a linear system, the only asymptotically stable solution is the zero-vector, i.e. when the population vanishes. If one is interested in conditions to maintain a (Lyapunov) stable non-vanishing population in the context of neutral competition, one must consider marginally stable solutions, a *steady state*, which is not as strictly controlled as asymptotically stable systems but does not diverge nor vanish.

Another example of linear cooperative systems where the marginally stable state is of high interest are Markov processes: a Markov process' Master equation represents a linear cooperative system since stochastic transition rates are non-negative. Thus, the steady state solution of such a Master equation is a marginally stable state of the corresponding Master equation. Nonetheless, due to the conservation of probability, this marginally stable *steady state* resists perturbations, thus all allowed perturbations are within the steady states' stable subspace.

In this article we find conditions for the stability of linear cooperative systems of a positive quantity, based on graphical criteria of the underlying dependence graph. In particular, we find how marginal stability can be determined by decomposing the system into its strongly connected components (SCCs). The stability can then be inferred from (i) the spectrum of the Jacobian matrix of isolated SCCs, and (ii) the hierarchical arrangement of the SCCs. Our main result is Theorem 3 (illustrated in Fig. 2) which states that for (marginal) stability to prevail, no SCC may have positive eigenvalues, and any SCCs with eigenvalue zero may not stand in any hierarchical relation to each other, i.e. there may be no (directed) path connecting them. This reflects the principle that the larger and more connected complex systems are, the more likely they are to become unstable [9].

2 Results

We consider a generic cooperative linear dynamical system of a positive quantity ('mass') m on a directed weighted graph with n nodes, whereby we denote $m_i = m_i(t)$ as the mass fraction on node $i = 1, ..., n$ at time t. The state vector of the system is $\mathbf{m} = (m_1, m_2, ..., m_n)^T$ and the system is written as

$$\frac{d}{dt}\mathbf{m}(t) = A\,\mathbf{m}(t) \tag{1}$$

for a $n \times n$ real square matrix

$$A = [a_{ij}], \text{ with } a_{ij} \geqslant 0 \text{ for } i \neq j. \tag{2}$$

The condition $a_{ij} \geqslant 0$ for $i \neq j$, defines the system as *cooperative*, since A is the Jacobian matrix of the system (1).

We consider the underlying directed weighted graph $G(A)$ with transposed adjacency matrix A, that is, the graph with n nodes and a link from j to i, weighted by a_{ij}, only if $a_{ij} \neq 0$. This is a finite simple graph with positively weighted edges and arbitrarily weighted self-loops. We wish to relate the stability of the fixed points of (1) to the network structure of $G(A)$.

Since A is the Jacobian of (1), the stability of a fixed point $\mathbf{m}^*$, defined by $A\,\mathbf{m}^* = \mathbf{0}$ (that is, a 0-eigenvector of A), is determined by the spectral properties of A. For the system to be asymptotically stable, all the real parts of the eigenvalues of A must be negative. In this case, however, $\det(A) \neq 0$ and the only fixed point $A\,\mathbf{m}^* = \mathbf{0}$ is trivial, $\mathbf{m}^* = \mathbf{0}$. As we are interested in non-trivial solutions, we focus instead on Lyapunov stable fixed points which are at least marginally stable (also called *semi-stable* [3]). This is the case if the eigenvalue of A with largest real part is zero and its geometric multiplicity is equal to its algebraic multiplicity [10]. Our main result is a necessary and sufficient condition on the structure of the graph $G(A)$, for the dynamical system to have non-trivial, marginally stable, non-negative solutions. Note that we call a vector $\mathbf{m}$ (or, similarly, a matrix) *non-negative*, written $\mathbf{m} \geqslant 0$, if all entries are real and non-negative, and *positive*, written $\mathbf{m} > 0$, if all entries are real and positive.

First, we decompose $G(A)$ into its strongly connected components, as follows. A (sub-)graph is *strongly connected* if for any pair of nodes i and j in the graph there is a directed path from i to j and a directed path from j to i, that is, every pair of nodes is mutually reachable. Every directed graph can be partitioned into maximal strongly connected subgraphs, the graphs *strongly connected components* (SCCs). The SCCs of a directed graph G form another graph called the *condensation* of G: in it, each node represents an SCC, and if two SCCs in G are connected by at least one link, then the condensation possesses a link between them, in the same direction as in G (see Fig. 1). The condensation of a directed graph is always a directed acyclic graph and, hence, its nodes (the SCCs of G) admit a *topological ordering* [11]: an ordering $B_1, B_2, \ldots, B_h$ (from now on, we will identify the kth connected component of G with its adjacency matrix B_k) such that if there is a link from B_i to B_j then $i \leqslant j$ (see Fig. 1 for an example). We can extend the ordering to the nodes of G so that node $u \in B_i$ appears before node $v \in B_j$ whenever $i \leqslant j$. With respect to this this re-ordering and re-labelling of the nodes of G, the adjacency matrix A of $G(A)$ becomes a lower triangular matrix

$$A = \begin{pmatrix} B_1 & 0 & 0 & 0 & \ldots \\ C_{21} & B_2 & 0 & 0 & \ldots \\ C_{31} & C_{32} & B_3 & 0 & \ldots \\ \vdots & \vdots & \vdots & \ddots & 0 \\ \ldots & \ldots & \ldots & \ldots & B_h \end{pmatrix}, \tag{3}$$

where h is the number of SCCs of $G(A)$, B_k is the adjacency matrix of the k-th SCC ($1 \leqslant k \leqslant h$), and C_{kl} encodes the connectivity from B_l to B_k. This is sometimes called the *normal form of a reducible matrix* [12]. If there exist a path from k to l (thus $k \leqslant l$), we call B_k *upstream* of B_l, and B_l is *downstream* of B_k. If B_k is connected by a single (directed) link to B_l then we also call B_k *immediately upstream* of B_l, and B_l *immediately downstream* of B_k. From now on, we will implicitly assume a topological sorting and notation as above.

Since A, written in the form (3), is a lower triangular block matrix, the characteristic polynomial of A, $p_A(\lambda) = \det(\lambda I - A)$, is the product of the characteristic polynomials of the B_k's

$$p_A(\lambda) = p_{B_1}(\lambda) \cdot \ldots \cdot p_{B_h}(\lambda). \tag{4}$$

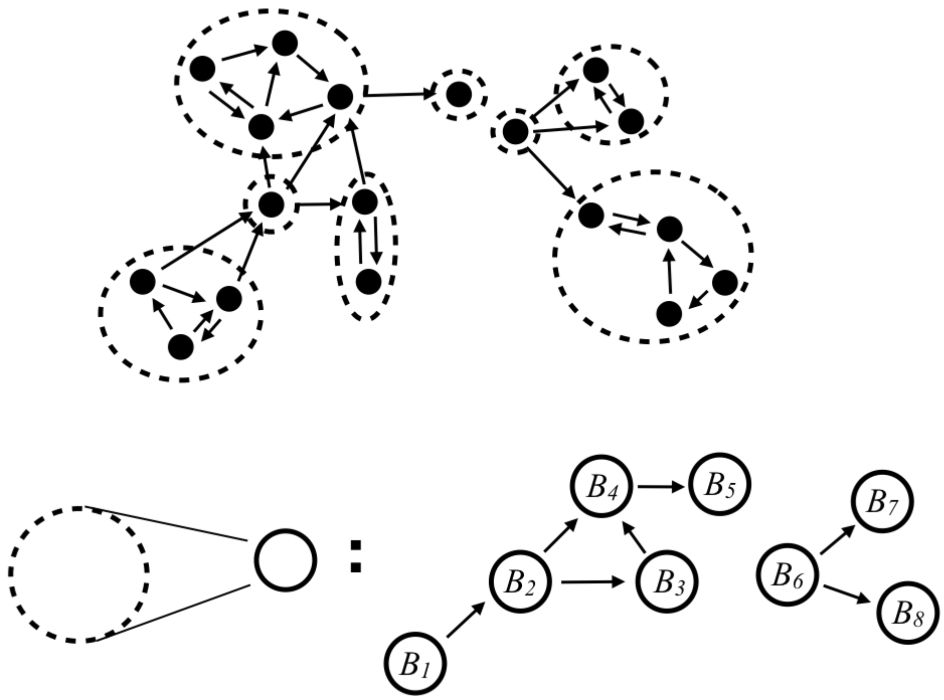

Figure 1: Decomposition of a directed graph into SCCs and its condensation graph. (Top) A directed graph (black dots represent nodes, and arrows directed links) and its SCCs (dashed circles). Note that every node belongs to a SCC, and that a SCC can be a single node. (Bottom) Condensation of the directed graph: black circles represent the SCCs and arrows whenever two SCCs are connected via *at least* one link (in the direction shown). The condensation of a graph is always a directed acyclic graph and hence admits a topological ordering, shown here as B_1 to B_8.

Thus the spectrum of A – seen as a multiset – is the union of the spectra of the B_k's, and the algebraic multiplicity of the eigenvalues is preserved.

Since all off-diagonal elements of A (and hence of each B_k) are non-negative, and each B_k is the adjacency matrix of a strongly connected graph, the matrices B_k are irreducible Metzler matrices, for which the Perron-Frobenius Theorem applies, to the shifted eigenvalues [13]. Therefore, each matrix B_k has a real eigenvalue μ_k with (strictly) largest real part, which is simple and has a positive eigenvector $\mathbf{m} > 0$. We call μ_k the *dominant eigenvalue* of the matrix B_k.

We now introduce some further terminology. We call each SCC, and equivalently its adjacency matrix B_k, a *block* of the system (we use the term 'block' and the notation B_k for both the matrix and its graph). We call a block *critical* if its dominant eigenvalue $\mu_k = 0$, *sub-critical* if $\mu_k < 0$ and *super-critical* if $\mu_k > 0$. Correspondingly, we define the index subsets $I_c = \{k \in 1, ..., h \mid B_k \text{ critical}\}$, $I_s = \{k \in 1, ..., h \mid B_k \text{ sub-critical }\}$, $I_{sp} = \{k \in 1, ..., h \mid B_k \text{ super-critical }\}$. The first things we note are (see for example [8]) are

Lemma 1. *If at least one block B_k of A is super-critical, then the system (1) is unstable.*

Lemma 2. *The system (1) is asymptotically stable if and only if all blocks B_k of A are sub-critical.*

These Lemmas follow immediately from the the fact that a system is unstable if at least one real part of an eigenvalue of A is positive and it is asymptotically stable if and only if all real parts of eigenvalues are negative, together with the property that the spectrum of A is the multi-set union of spectra of the B_k (note, however, that the 'if and only if' statement only holds for Lemma 2). In the situation of Lemma 2, observe that $\det(A) \neq 0$ and hence $\mathbf{m}^* = \mathbf{0}$ is the only fixed point of the system.

Lemmas 1 and 2 cover all cases where any super-critical blocks exist, or only sub-critical ones. In these cases, the system is either unstable, or has only a trivial (zero) fixed point. In the following, we will consider only the remaining cases when no super-critical blocks exist, but there is at least one critical block, and investigate the existence of non-trivial, non-negative (so that each node supports a non-negative fraction of the 'mass') marginally stable fixed points.

If no super-critical, and at least one critical, block exists, the dominant eigenvalue of A is zero and, according to the Perron-Frobenius theorem, there exist non-trivial eigenvectors $\mathbf{m}^*$ for the eigenvalue zero. It is assured that all such $\mathbf{m}^*$ are equilibrium points of the system (1), however, to be a (Lyapunov) stable equilibrium it is required that the algebraic multiplicity of eigenvalue zero is equal to its geometric one, or equivalently, equal to the dimension to the nullspace of A. We will approach the latter question by explicitly constructing such equilibrium sets.

Let us first write the equilibrium condition of the dynamical system (1), using (3), as

$$\begin{pmatrix} B_1 & 0 & 0 & 0 & ... \\ C_{21} & B_2 & 0 & 0 & ... \\ C_{31} & C_{32} & B_3 & 0 & ... \\ \vdots & \vdots & \vdots & \ddots & 0 \\ ... & ... & ... & ... & B_h \end{pmatrix} \begin{pmatrix} \mathbf{m}_1^* \\ \mathbf{m}_2^* \\ \mathbf{m}_3^* \\ \vdots \\ \mathbf{m}_h^* \end{pmatrix} = 0, \tag{5}$$

i.e. the equilibrium vector $\mathbf{m}^*$ is decomposed in the projections $\mathbf{m}_k^*$ on the sub-space of B_k, in the form $\mathbf{m}^* = (\mathbf{m}_1, \mathbf{m}_2, ..., \mathbf{m}_h)^T$. For simplicity, we call $\mathbf{m}_k^*$ the *steady state on* B_k. We further call a block B_k *trivial* if $\mathbf{m}_k^* = \mathbf{0}$ for all non-negative marginally stable fixed points $\mathbf{m}^*$ of the system (5), and *non-trivial* otherwise[1]. In other words, a trivial block is one that does not support any positive fraction of the 'mass' for any non-negative fixed point.

Our first result is a formula for the steady states $\mathbf{m}_k^*$ on sub-critical blocks B_k. Let us consider the k-th row of (5),

$$\sum_{l<k} C_{kl}\, \mathbf{m}_l^* + B_k \mathbf{m}_k^* = 0 \tag{6}$$

where B_k is a sub-critical block. Since all eigenvalue real parts of B_k are negative, $\det(B_k) \neq 0$ and thus B_k is invertible, so that we obtain a recursive formula for the steady state:

$$\mathbf{m}_k^* = -B_k^{-1} \left[\sum_{l<k} C_{kl}\, \mathbf{m}_l^* \right]. \tag{7}$$

[1]Note that $\mathbf{m}_k^*$ is the k-th subspace component of the global steady state $\mathbf{m}^*$ of A, but not necessarily the steady state of the isolated subsystem of B_k.

Let $I_f \subseteq I_c$ denote the indices of the critical SCCs for which there are no other critical SCCs downstream. Let us call them *final critical SCCs*. With this terminology, we have, from the recursion relation above, the following:

Theorem 1. *If B_k is a sub-critical block of A and Eq. (5) holds, then $\mathbf{m}_k^*$, the steady state on B_k, is uniquely determined by the final critical blocks upstream of B_k, namely*

$$\mathbf{m}_k^* = -B_k^{-1} \left[\sum_{l \in I_f} P_{kl} \, \mathbf{m}_l^* \right], \tag{8}$$

where

$$P_{kl} = \sum_{(l_1, l_2, \ldots, l_n) \in \mathcal{P}_{kl}} (-1)^{n-1} C_{kl_1} B_{l_1}^{-1} C_{l_1 l_2} B_{l_2}^{-1} \cdots C_{l_n l} \tag{9}$$

and $\mathcal{P}_{kl}$ is the set of all paths from B_l ($l \in I_f$) to B_k, written as a sequence of nodes $(l_1, l_2, \ldots, l_n)$, where n is the length of the path.

This follows directly if we apply the relation Eq. (7) recursively to all steady states $\mathbf{m}_k^*$ of sub-critical blocks B_k on the right hand side of Eq. (7), using that when propagating upstream, no critical SCCs can be encountered before a final critical SCC is encountered.

Theorem 1 assures that the steady state on any sub-critical block is uniquely defined by the steady states on all critical blocks upstream of the former. Furthermore, we can conclude:

Corollary 1. *If B_k is a sub-critical block of A, then B_k is trivial if and only if all B_l immediately upstream of B_k are trivial.*

Proof. From Eq. (7) it directly follows that if all B_l immediately upstream are trivial ($\mathbf{m}_l^* = 0$), then B_k is trivial ($\mathbf{m}_k^* = 0$). Now let us consider the case that at least one B_l immediately upstream has $\mathbf{m}_l^* \neq 0$. We first note that since B_k is a Metzler matrix with $\det(B_k) \neq 0$, $-B_k$ is a non-singular M-matrix, and its inverse is a positive matrix (shown in [14]). Thus $\mathbf{m}_k^*$ is positive if at least one $\mathbf{m}_l^* \neq 0$ (recall that $\mathbf{m}^*$ and the C_{kl}'s are non-negative). Therefore it follows: if B_k is trivial, i.e. $\mathbf{m}_k^* = 0$, then for all immediately upstream B_l, $\mathbf{m}_l = 0$, and hence B_l is trivial. □

Now we make a topological characterisation of the trivial blocks.

Theorem 2. *A block is trivial if and only if*

(i) it is upstream of a critical block, or

(ii) it is a sub-critical block which is not downstream of a critical block.

Thereby all trivial blocks can be easily identified by inspecting the condensed graph and its critical blocks (Fig. 1).

Proof. To prove Theorem 2, consider an equilibrium point $\mathbf{m}^*$. Then Eq. (5) holds, and in particular its k-th row Eq. (6). Now B_k is critical and hence has an eigenvalue zero ($\mu_k = 0$ by definition), $\det(B_k) = 0$ and thus B_k is not invertible. Let us multiply both sides of Eq. (6) with the matrix exponential $e^{B_k t} = \sum_{n=1}^{\infty} \frac{(B_k t)^n}{n!}$ to yield,

$$e^{B_k t} B_k \mathbf{m}_k^* = B_k \left[e^{B_k t} \mathbf{m}_k^* \right] = -e^{B_k t} \left[\sum_{l<k} C_{kl} \mathbf{m}_l^* \right] \quad , \tag{10}$$

where we used that for a square matrix M commutes with its exponential, $e^M M = M e^M$. In general, $e^{Mt}\mathbf{m}$ is a solution of the linear ODE $\dot{\mathbf{x}} = M\mathbf{x}$ and thus converges to a linear combination of dominant eigenvectors (eigenvectors of the dominant eigenvalues) of M. Since B_k is critical, the corresponding dominant eigenvalue is zero and thus $B_k[e^{B_k t}\mathbf{m}_k^*] \to 0$ for $t \to \infty$. This means that $-e^{\mathcal{B}_k t}[\sum_{l<k} C_{kl}\mathbf{m}_l^*] = 0$ for $t \to \infty$ and, since the matrix exponential is always invertible, we can conclude that $\sum_{l<k} C_{kl}\mathbf{m}_l^* = 0$. Note that all entries of the matrices C_{kl} and of the vector $\mathbf{m}_l^*$ are non-negative, so this can only be the case if, for all $l < k$, $C_{kl} = 0$ or $\mathbf{m}_l^* = \mathbf{0}$. Since, for all immediately upstream blocks, we have $C_{kl} \neq 0$, it follows that

Lemma 3. *All blocks immediately upstream of a critical block are trivial.*

Crucially, from Theorem 1 and Lemma 1, it follows that all blocks B_m immediately upstream of any trivial block B_l are trivial (either B_l is critical, or sub-critical and trivial). By applying this argument recursively to Lemma 1, the first part of Theorem 2 follows. The second part is an immediate consequence of Corollary 1. □

We can also easily follow from Theorem 2 and Eq. (10):

Corollary 2. *The steady states $\mathbf{m}_k^*$ on a non-trivial critical block B_k (called a* free *block) is the one-dimensional family of dominant eigenvectors (of eigenvalue zero) of B_k. We can write these as $\alpha_k \boldsymbol{\phi}_k$ where $\alpha_k \in \mathbb{R}$ is a free parameter, and $\boldsymbol{\phi}_k$ is a (normalised) dominant eigenvector of B_k.*

Theorems 1 and 2, and Corollary 2, allow us to construct the most generic steady state of the system (1), that is, the nullspace of A. From Theorem 2, it follows that the set of non-trivial SCCs is exactly the set of *final* SCCs, as defined before Theorem 1. Hence $I_f \subseteq I_c$ is also the index set of non-trivial critical blocks, that is, $I_f = \{1 \leqslant k \leqslant h \mid B_k \text{ critical and non-trivial}\}$. All in all, a steady state vector $\mathbf{m}^* = (\mathbf{m}_1, \mathbf{m}_2, ..., \mathbf{m}_h)^T$ has the form

$$\mathbf{m}_k^* = \begin{cases} 0 & \text{if} \quad B_k \text{ is upstream of any critical block,} \\ \alpha_k \boldsymbol{\phi}_k & \text{if} \quad k \in I_f, \\ B_k^{-1}\left[\sum_{l \in I_f} P_{kl} \alpha_l \boldsymbol{\phi}_l\right] & \text{if} \quad B_k \text{ is sub-critical.} \end{cases} \tag{11}$$

This can also be written as

$$\mathbf{m}^* = \sum_{k \in I_f} \alpha_k \mathbf{m}^{*(k)}, \text{ with } \mathbf{m}_l^{*(k)} = \begin{cases} 0 & \text{if} \quad B_l \text{ is upstream of } B_k, \\ 0 & \text{if} \quad l \in I_f \text{ and } l \neq k, \\ \boldsymbol{\phi}_k & \text{for} \quad l \in I_f, \\ B_l^{-1}\left[P_{lk} \boldsymbol{\phi}_k\right] & \text{if} \quad B_l \text{ is sub-critical.} \end{cases} \tag{12}$$

Hence, the dimension of the nullspace of A (equivalently, the geometric multiplicity of the eigenvalue zero) is equal to the number of non-trivial critical blocks. The algebraic multiplicity, on the other hand, is the number of all critical blocks, since according to the Perron-Frobenius Theorem for Metzler matrices, each critical block has a simple (algebraic multiplicity 1) eigenvalue zero and thus contributes once to the multiset of eigenvalues of A, by Eq. (4). Recall that the system (1) is marginally stable if and only if the dominant eigenvalue of A is zero and its geometric multiplicity is equal to the algebraic multiplicity; this is thus the case only if there are no super-critical blocks and all critical blocks are non-trivial. According to Theorem 2, this is the case if no critical block is upstream of another critical block, or alternatively, if there are no paths between any two critical blocks. We thereby arrive at

Theorem 3. *A dynamical system in the form of Eq. (1) with Jacobian matrix A is marginally stable if these conditions hold:*

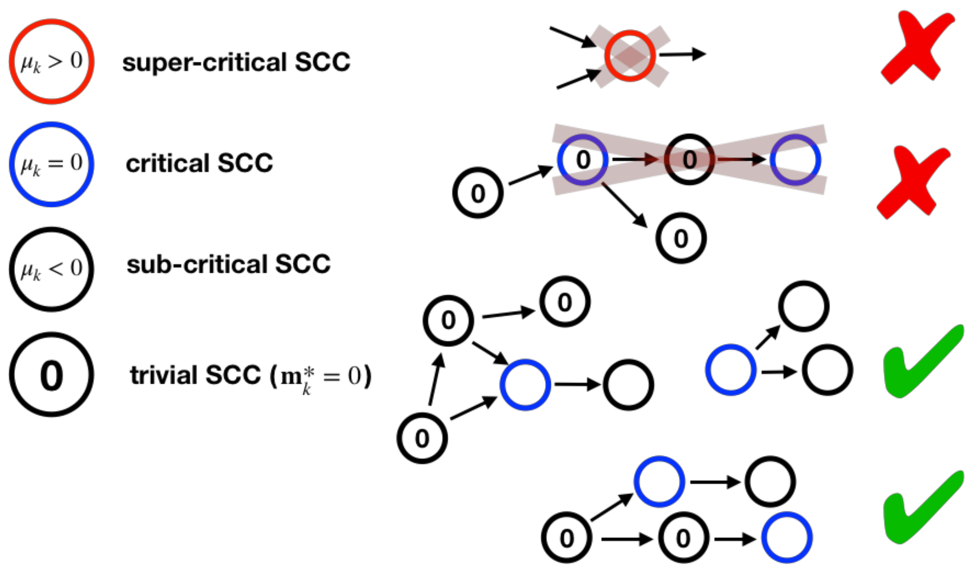

Figure 2: Illustration of Theorem 3. Circles are SCCs, according to the condensation mapping as illustrated in Fig. 1 and coloured according to their type. For a linear cooperative system to be stable, all SCCs must have non-positive eigenvalues (no super-critical SCCs), and any SCCs with dominant eigenvalue zero (critical SCCs) cannot be connected by any directed path. Configurations which allow marginally stable states are shown with a green tick, and those which are unstable with a red cross. For the former, we also mark the trivial blocks. All non-negative, marginally stable states can be determined by setting zero all the nodes in all the trivial blocks, choose one 0-eigenvector for each critical (blue) block, and propagate them downstream using Eqs. (9) and (8).

(a) there are no super-critical blocks;

(b) there is at least one critical block;

(c) there are no (directed) paths in $G(A)$ which connect two critical blocks.

Part (a) and (b) follow from Lemmas 1 and 2, while part (c) follows from Eq. (12). This theorem is illustrated in Fig. 2. To summarise our findings, including the necessary definitions, we can express the stability criteria of cooperative dynamical systems as

Theorem 4. *Let $A = [a_{ij}]$, with $a_{ij} \geqslant 0$ if $i \neq j$, be the Jacobian matrix of the cooperative system in Eq. (1), and $G(A)$ its weighted graph, defined by the edge weights a_{ij} for all i, j. Let $B_1, \ldots, B_h$ be the adjacency matrices of the strongly connected components (SCCs) of $G(A)$. We define an SCC as* critical *if its dominant eigenvalue is zero,* sub-critical, *if its dominant eigenvalue is negative, and* super-critical *if its dominant eigenvalue is positive. Then:*

1. *The system is asymptotically stable if and only if all SCCs are sub-critical.*
2. *Otherwise, the system is marginally stable if*
   (a) *there are no super-critical SCCs, and*
   (b) *there are no paths in $G(A)$ which connect two critical SCCs.*
3. *Otherwise, the system is unstable.*

The corresponding equilibrium set of the system is given by Eq. (11).

3 Application: Stochastic processes

A prominent class of linear cooperative systems – although rarely seen as such – are *Markov processes* [2]. They can be mathematically represented by the chemical Master equation which describes the time evolution of the probability distribution. Denoting by $\mathbf{P} = (P_1, P_2, ..., P_N)$ the probabilities to be in states $i = 1, 2, ..., N$ of a *finite* Markov process (with a finite number of states), the Master equation is,

$$\dot{\mathbf{P}}(t) = A\mathbf{P}(t) \tag{13}$$

where $A = [a_{ij}]$ satisfies $\sum_j a_{ij} = 0$ to ensure the conservation of probability. The off-diagonal elements of A are the stochastic transition rates and the diagonal elements are such that they ensure the conservation property, $a_{jj} = -\sum_{i \neq j} a_{ij}$. Since the stochastic rates are non-negative, $a_{ij} \geqslant 0$ for $i \neq j$, this is a linear cooperative system for the probability distribution

[2]Note that here we use the term Markov *process* for stochastic processes with Markov property in continuous time, in contrast to a Markov *chain*, which denotes stochastic processes with Markov property in discrete time. The terminolology varies in the literature.

$\mathbf{P}(t)$. Notably, by applying Theorem 4 and the Perron-Frobenius theorem to stochastic systems, some well-known core results for finite Markov processes can be easily found.

For that purpose we note the following:

1. Since $\sum_i a_{ij} = 0$, for each block $B_k = [b_{ij}^{(k)}]$ in the representation (3), we have $\sum_i b_{ij}^{(k)} \leqslant 0$. According to the Perron-Frobenius theorem, $\min_j \left(\sum_i b_{ij}^{(k)}\right) \leqslant \nu_k \leqslant \max_j \left(\sum_i b_{ij}^{(k)}\right)$, where ν_k is the dominant eigenvalue, hence $\nu_k \leqslant 0$ and thus there cannot be any supercritical blocks.

2. For j in the last block, B_m, $\sum_i b_{ij}^{(m)} = \sum_i a_{ij} = 0$, so at least that block is critical.

3. No critical block can have an outgoing edge, otherwise $\sum_i a_{ij} > \sum_i b_{ij}^{(k)} \geqslant 0$, which contradicts $\sum_i a_{ij} = 0$.

From points 1-3 follows that the requirements for Theorem 4 are fulfilled and thus that any finite Markov process has a marginally stable state. In that case, due to the conservation law $\sum_i P_i = 1$, this marginally stable state is in fact a steady state. Furthermore, we can use Eqs. (11,12) to construct these states and we immediately see that a finite Markov process has a unique steady state exactly if there is only a single critical block. If there are further blocks upstream of that critical block, those must be trivial, with $P_i = 0$. Yet, even if the steady state is unique, the Markov process is non-ergodic if there is more than one SCC. On the other hand, a finite Markov process is ergodic if and only if the graph of A represents a single SCC. Hence, our analysis allows to conclude some fundamental results on stochastic systems in a very simple way.

4 Conclusions

Theorem 4 prescribes a way to simplify the analysis of a high-dimensional linear cooperative system by decomposing it into lower dimensional subsystems, the dynamical graph's strongly connected components (SCCs). By spectral analysis of these SCCs and checking whether the conditions of theorem 4 are fulfilled, the systems stability can be determined. In particular, *marginal stability* is of importance for linear systems, since marginally stable states represent the only possible non-trivial stable steady states. In contrast, asymptotically stable states are trivially vanishing. Moreover, our analysis revealed a formula (Eqs. (11,12)) to construct the steady state only by the knowledge of the steady states on the critical strongly connected components, i.e. those with dominant eigenvalue zero.

The theorem can be applied to a wide range of systems: *compartmental systems*, where the dynamics are defined by transitions of a positive quantity between certain compartments, which may reflect spatial compartments or any kind of states or dynamical stages of that quantity. If there are no explicit interactions between compartments, the dynamics are linear and cooperative, since transition rates are always non-negative. Also *population dynamics* are cooperative, and where individuals transit between different stages can be seen as generalised compartmental dynamics. An example are populations of stem cells in animal tissues which differentiate, thereby changing their cell type. While populations as a whole are often subject to feedback and thus follow non-linear dynamics, when considering a subpopulation therein, which compete neutrally, the corresponding subsystem is linear.

Furthermore, we showed that all finite Markov processes are linear cooperative systems, and by applying theorem 4, some of the most fundamental results known about Markov processes follow in an immediate and elegant way, namely that (i) every finite Markov process has a steady state, (ii) this steady state is unique if and only if there is only one critical SCC in the underlying graph, and (iii) a finite Markov process is ergodic exactly if the underlying graph as a whole is strongly connected.

In general, stochastic and other cooperative systems can be highly complex, with a large number of variables and very complex interactions, hence represented by large and often irregular graphs. The method presented here is a way to significantly simplify the analysis of a wide range of systems, ranging from stochastic processes to compartmental dynamics, by decomposing the systems into its strongly connected components. We have shown that a spectral analysis of each SCC, and a simple graphical criterion of the connectivity between SCCs (Theorem 4, Figure 2) completely determines the stability of any cooperative system. This provides a unique insight into the possible configurations of cooperative systems and demonstrates the power of graph theoretic techniques in the analysis of complex dynamical systems.

References

[1] M. W. Hirsch and H. Smith. Monotone dynamical systems. *Handbook of differential equations: Ordinary Differential Equations*, pages 239–357, 2005.

[2] G. Kron. *Diakoptics*. MacDonald, 1963.

[3] W. M. Haddad, V. S. Chellaboina, and Q. Hui. *Nonnegative and Compartmental Dynamic Systems*. Princeton Unversity Press, 2010.

[4] Robert M. May. Qualitative stability in model ecosystems. *Ecology*, 54:638–641, 1973.

[5] K. Godfrey. *Compartmental models and their application*. Academic Press, 1983.

[6] Herbert W Hethcote. The Mathematics of Infectious Diseases. *SIAM Review*, 42(4):599–653, 2000.

[7] P. Greulich and B. D. Simons. Dynamic heterogeneity as a strategy of stem cell self-renewal. *Proceedings of the National Academy of Sciences*, 113:7509, 2016.

[8] A. K. Kevorkian. Structural Aspects of Large Dynamic Systems. *IFAC Proceedings Volumes*, 8(1):101–111, 1975.

[9] Robert M. May. Will a large complex system be stable? *Nature*, 238(5364):413–414, 1972.

[10] K J Åström and Richard M Murray. *Feedback Systems: An Introduction for Scientists and Engineers*. Princeton University Press, 2008.

[11] Thomas H Cormen, Charles E Leiserson, Ronald L Rivest, and Clifford Stein. *Introduction to algorithms*. MIT press, 2009.

[12] R. S. Varga. *Matrix Iterative Analysis*. Springer, 2000.

[13] C R MacCluer. The Many Proofs and Applications of Perron's Theorem. *SIAM Review*, 42(3):487–498, 2000.

[14] C. D. Meyer and M. W. Stadelmeier. Singular M-Matrices and Inverse Positivity. *Linear Algebra and Its Applications*, 22, 1978.