Impact of network connectivity on the synchronization and global dynamics of coupled systems of differential equations

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HIGHLIGHTS

- We investigated a general class of coupled dynamical systems on networks.
- We established the global dynamics when the network is not strongly connected.
- We investigated the impact of network connectivity on the global dynamics.
- When vertex systems are gradient, network connectivity completely determines the synchronization.
- We applied the theory to two significant applications in epidemiology and ecology.

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ABSTRACT

The global dynamics of coupled systems of differential equations defined on an interaction network are investigated. Local dynamics at each vertex, when interactions are absent, are assumed to be simple: solutions to each vertex system are assumed to converge to an equilibrium, either on the boundary or in the interior of the feasible region. The interest is to investigate the collective behaviours of the coupled system when interactions among vertex systems are present. It was shown in Li and Shuai (2010) that, if the interaction network is strongly connected, then solutions to the coupled system synchronize at a single equilibrium. We focus on the case when the underlying network is not strongly connected and the coupled system may have mixed equilibria whose coordinates are in the interior at some vertices while on the boundary at others. We show that solutions on a strongly connected component of the network will synchronize. Considering a condensed digraph by collapsing each strongly connected component, we are able to introduce a partial order on the set $\mathcal{P}$ of all equilibria, and show that all solutions of the coupled system converge to a unique equilibrium P^* that is the maximizer in $\mathcal{P}$. We further establish that behaviours of the coupled system at minimal elements of the condensed digraph determine whether the global limit P^* is a mixed equilibrium. The theory are applied to mathematical models from epidemiology and spatial ecology.

1. Introduction

Coupled systems on networks is a mathematical framework that encompasses many different classes of large-scale artificial and natural systems [1]. A network is given by a weighted digraph $(\mathcal{G}, A)$, where $\mathcal{G}$ is a digraph with vertex set $V(\mathcal{G}) = \{1, 2, \ldots, n\}$, and $A = (a_{ij})_{n \times n} \geq 0$ is the weight matrix. At each vertex i, a differential system $u_i' = f_i(u_i)$ is defined. Inter-connections or coupling among vertex systems are described by the edges of $\mathcal{G}$, and the strength of the coupling described by the weights of edges.

In particular, an edge (i, j) from vertex j to i exists if and only if $a_{ij} > 0$. A coupled system defined on a network $(\mathcal{G}, A)$ can be written in the form

$$u_i' = f_i(u_i) + \sum_{j=1}^{n} a_{ij} g_{ij}(u_i, u_j), \quad i = 1, 2, \ldots, n, \tag{1}$$

and $g_{ij}(u_i, u_j)$ is a normalized interference function from vertex j to i [1]. System (1) can describe a network of coupled oscillators in which each vertex system is an oscillator and g_{ij} describe the coupling terms. System (1) can also model the flocking of birds, swarms of aerial robots and formation of small satellites, for which $(\mathcal{G}, A)$ describes the communication topology. For ecological systems with spatial dispersal, vertex systems in (1) may model the

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dynamics of species on a single patch, g_{ij} describes the dispersal term and $(\mathcal{G}, A)$ is the dispersal network.

Many mathematical questions can be investigated in the framework of coupled systems on networks. Each vertex system is typically of low dimension and whose dynamics are simple. Assuming that each vertex system has a global attractor that is an equilibrium or a limit cycle, one can ask if the coupled system has a unique equilibrium or limit cycle and if it is globally attracting. The framework is also a natural setting for investigating the emergence of complex patterns and system behaviours from organization of simple dynamics. Of key interest is the impact of network structure, whether geometrical, topological or graph theoretical, on the system behaviours. In this study, we are interested in the impact of network connectivity on the simplest type of invariant sets: the set of equilibria. A motivation for this study comes from modelling of the transmission dynamics of infectious diseases within a heterogeneous host population in mathematical epidemiology. Multi-group models have been used to model heterogeneous transmission of sexually transmitted diseases [2]. A main mathematical question regarding the global dynamics is the threshold theorem: if the basic reproduction number $R_0 \leq 1$ then the unique disease-free equilibrium P_0 is globally stable and the disease dies out; if $R_0 > 1$ then P_0 is unstable and the disease persists. In particular, a unique endemic equilibrium P^* exists and is globally stable with respect to all positive initial conditions. Multigroup models is an example of couple systems on networks in which the network $(\mathcal{G}, A)$ describes cross-transmission among groups. The uniqueness and global stability of the endemic equilibrium for an n-group SIR model with bilinear incidence was first established in [3] using a global Lyapunov function, under the assumption that the cross-transmission network is strongly connected, or in biological terms, if the disease can be transmitted from one group to another group either directly or indirectly through other groups. Using the same technique, the threshold theorem is established for many other heterogeneous epidemic models structured with groups [4,5], infection stages [6] and spatial dispersal [7]. The overarching assumption for these threshold results is that the underlying network is strongly connected. On the other hand, threshold results for heterogeneous epidemic models are not expected to hold when the network is not strongly connected. It is shown in [8] that mixed equilibria, at which some group/patch is disease-free while others are endemic, can exist if the network is not strongly connected. Further studies are needed to investigate the global dynamics of heterogeneous epidemic models without the assumption of strong connectedness, and address the following questions: what are the structures of the set of equilibria? Can a mixed-equilibrium attract all positive solutions, and if so, how to characterize and identify the global attracting equilibrium?

In the present paper, in the general mathematical framework of coupled systems on networks (1), we investigate the structure of the set of equilibrium without the strong connectedness assumption on $\mathcal{G}$. We show that on each strongly connected component H of $\mathcal{G}$ the behaviour of system (1) tends to be synchronized, the equilibrium is either positive or zero at all vertex in H. This allows us to consider a condensed graph $\mathcal{H} = \mathcal{G}/\sim$ by collapsing each strongly connected component to a single vertex. A canonical partial order $\prec$ can be defined on the condensed graph $\mathcal{H}$, which encodes the structure of the set of equilibria. We define an evaluation function E on the ordered condensed graph $(\mathcal{H}, \prec)$, and show that E has a unique maximizer P^*, and that P^* corresponds to a unique equilibrium of (1), either positive or mixed, that attracts all positive solutions.

We present our main theoretic results in Section 2. In Sections 3 and 4, we apply our general approach to well-known examples of coupled systems. In Section 5, we present numerical examples to demonstrate our main results. Numerical simulations of a network of three coupled oscillators are also given in Section 5, to demonstrate the importance of network connectivity on synchronous oscillatory behaviours.

2. Coupled systems on networks

Let $\mathcal{G}$ be a digraph of n vertices. Consider a coupled system on graph $\mathcal{G}$ of form:

$$u_i' = f_i(u_i) + \sum_{j=1}^{n} g_{ij}(u_i, Pu_j), \quad i = 1, 2, \ldots, n, \quad (2)$$

where $u_i \in \mathbb{R}^d$, $f_i = (f_i^1, f_i^2, \ldots, f_i^d) : \mathbb{R}^d \to \mathbb{R}^d$, and $g_{ij} = (g_{ij}^1, g_{ij}^2, \ldots, g_{ij}^d) : \mathbb{R}^d \times \mathbb{R}^d \to \mathbb{R}^d$. Functions g_{ij} represent the influence of vertex j on vertex i, and an arc from vertex j to i exists if and only if $g_{ij}(u_i, Pu_j) \not\equiv 0$. Matrix P is a $d \times d$ projection matrix, namely $P^2 = P$, and we assume that rank $P = r > 0$. For each $1 \leq i \leq n$, Pu_i are referred to as coupling variables.

Without loss of generality, we assume that the coupling graph $\mathcal{G}$ is connected, since otherwise each connected component of $\mathcal{G}$ gives rise to an independent system and can be treated separately. We make the following general assumptions.

(A₁) For $\forall 1 \leq i \leq n, 1 \leq m \leq d$, $f_i^m(u_i)\big|_{u_i^m=0} \geq 0$; and $f_i^m(u_i)\big|_{u_i^m=0} = 0$ only if $Pu_i = 0$.

(A₂) For $1 \leq i, j \leq n$, $u_i, u_j \geq 0$, $Pg_{ij}(u_i, Pu_j) \geq 0$; if $Pg_{ij} \not\equiv 0$, then $Pg_{ij}(u_i, Pu_j) \neq 0 \Leftrightarrow Pu_j \neq 0$.

Assumption (A₁) requires that the vector field f_i is either tangent to or crosses each boundary subspace $u_i^m = 0$ of $\mathbb{R}_+^d$ to the interior. This ensures that the nonnegative orthant $\mathbb{R}_+^d$ is positively invariant for each vertex system $u_i = f_i(u_i)$, which is motivated by applications in population biology. Assumption (A₂) is regarding the non-negativity of the coupling term g_{ij}. We do not require that all entries in the vector g_{ij} to be nonnegative, and only that the coupling entries Pg_{ij} are nonnegative.

An equilibrium $u^* = (u_1^*, \ldots, u_n^*)$ is said to be *nonnegative* if it belongs to the nonnegative orthant $\mathbb{R}_+^d \times \cdots \times \mathbb{R}_+^d$ of the phase space. From assumption (A₁), we can deduce that at a nonnegative equilibrium u^*, for each vertex i, we have either $Pu_i^* > 0$ or $Pu_i^* = 0$, namely, there is no i such that vector Pu_i^* has both positive and zero coordinates. Equilibrium u^* is said to be *positive* if $Pu_i^* > 0$ for all i, and u^* is said to be *mixed* if there exist i, j such that $Pu_i^* = 0$ and $Pu_j^* > 0$. When matrix P has full rank, then $Pu_i^* > 0$ if and only if $u_i^* > 0$. In this case, a positive equilibrium belongs to the interior of the nonnegative orthant. Generally, if $Pu_i^* = 0$ for some i, then the equilibrium u^* belongs to the boundary of the nonnegative orthant, and is also called a boundary equilibrium. A mixed equilibrium is necessarily a boundary equilibrium, while a boundary equilibrium may not be mixed since we can have $Pu_i^* = 0$ for all i.

Define a partial order $\preceq$ among vertices of the digraph $\mathcal{G}$ as follows: for vertices i, j, $i \preceq j$ if there exists an oriented path from i to j. We say $i \sim j$ if $i \preceq j$ and $j \preceq i$. It can be verified straightforwardly that relation "$\sim$" is an equivalence relation.

Proposition 2.1. *Relation $\sim$ is an equivalence relation.*

Let $V(\mathcal{G})$ be the vertex set of digraph $\mathcal{G}$. Define $\mathcal{H}$ as the condensed graph of $\mathcal{G}$, which is formed by collapsing each strongly connected component to a single vertex. Then $V(\mathcal{H}) = V(\mathcal{G})/\sim$, and each vertex $H \in V(\mathcal{H})$ represents a strongly connected component of $\mathcal{G}$. If $\mathcal{G}$ is strongly connected, then $V(\mathcal{H}) = \{\mathcal{G}\}$ is a singleton. For $H, H' \in \mathcal{H}$, a directed edge from H to H' exists if there exist $i \in V(H)$ and $j \in V(H)$ such that a directed edge from i to j exists in $\mathcal{G}$. A canonical partial order $\prec$ can be defined in $\mathcal{H}$ as follows: for $H, H' \in V(\mathcal{H})$, $H \prec H'$ if there exist $i \in H, j \in H'$, such that $i \preceq j$. If $H, H' \in V(\mathcal{H})$ satisfy both $H \prec H'$ and $H' \prec H$, then H and H' are the same strongly connected component. This implies that $\prec$ is a strict partial order. Thus there exist minimal and maximal elements in $V(\mathcal{H})$ with respect to the strict partial order $\prec$ (see Fig. 1).
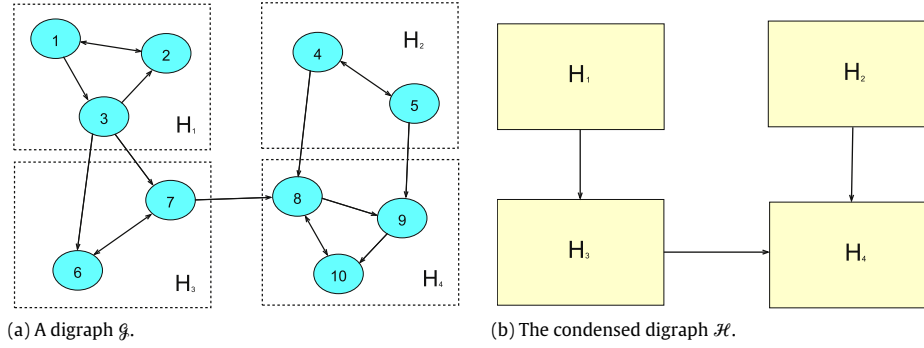
(a) A digraph $\mathcal{G}$.　　(b) The condensed digraph $\mathcal{H}$.

Fig. 1. A digraph $\mathcal{G}$, and its strongly connected components H_i are shown in (a). The corresponding condensed digraph $\mathcal{H}$ is shown in (b). H_1 and H_2 are minimal elements of $\mathcal{H}$.

For any $G \subseteq V(\mathcal{G})$, we denote

$$u_i' = f_i(u_i) + \sum_{j \in V(\mathcal{G})} g_{ij}(u_i, Pu_j), \quad i \in G \tag{3}$$

as the G-subsystem of system (2); and

$$u_i' = f_i(u_i) + \sum_{j \in G} g_{ij}(u_i, Pu_j), \quad i \in G \tag{4}$$

as the reduced G-subsystem of system (2);

For $H \in V(\mathcal{H})$ and $c = (c_1, c_2, \ldots, c_n) \geq 0$, where $c_i \in \mathbb{R}^d$, $1 \leq i \leq n$, we define

$$u_i' = f_i(u_i) + \sum_{j \in H} g_{ij}(u_i, Pu_j) + \sum_{l \in V(\mathcal{G}) \backslash H} g_{il}(u_i, Pc_l), \quad i \in H \tag{5}$$

as the restricted system of system (2) on H at c. The following result follows directly from these definitions.

Proposition 2.2. (a) If $H \in V(\mathcal{H})$ is a minimal element, then the H-subsystem is the same as the reduced H-subsystem.
(b) If $H \in V(\mathcal{H})$ is a maximal element, then the $V(\mathcal{G} \backslash H)$-subsystem is the same as the reduced $V(\mathcal{G} \backslash H)$-subsystem.
(c) When $c_l = 0$, $g_{il}(u_i, Pc_l) \equiv 0$, thus the restricted system becomes reduced H-subsystem.

A differential equation $x' = f(x)$, with $x = (x_1, \ldots, x_k) \in \mathbb{R}^k$, is said to be uniformly persistent in the nonnegative orthant $\mathbb{R}_+^k$ if (1) $\mathbb{R}_+^k$ is positively invariant, (2) solutions $x(t)$ with $x(0) > 0$ exist for all $t \geq 0$, and (3) there exists constant $c > 0$ such that $x(0) > 0$ implies

$$\liminf_{t \to \infty} x_i(t) > c, \quad i = 1, \ldots, k.$$

Uniform persistence concept is motivated by the co-existence of species in population biology. It implies that solutions in the interior of $\mathbb{R}_+^k$ stay away from the boundary in the limit [9,10].

We make the following additional assumptions on system (2).

(A_3) For $H \in V(\mathcal{H})$ and $c \geq 0$, the restricted system (5) on H at c has a nonnegative equilibrium that attracts all positive solutions.
(A_4) For $1 \leq i \leq n$, the vertex system $u_i' = f_i(u_i)$ has at most one boundary equilibrium.
(A_5) For $H \in V(\mathcal{H})$, if the reduced H-subsystem (4) has a positive equilibrium, then system (4) is uniformly persistent.

Assumption (A_3) is a key assumption that needs rigorous verification for each application. While the assumption may seem restrictive, its verification often relies on the property that a component H is strongly connected, and can take advantage of the method for constructing global Lyapunov functions on strongly connected networks developed in [4,11,6].

Theorem 2.3. Assume that (A_3) is satisfied. Then all positive solutions of coupled system (2) converge to the same nonnegative equilibrium P^*.

Proof. We use induction on the order $|V(\mathcal{H})|$ of $V(\mathcal{H})$. When $|V(\mathcal{H})| = 1$, system (5) is the same as (2), the theorem holds trivially. Assume that the theorem holds when $|V(\mathcal{H})| = m$. Then, when $|V(\mathcal{H})| = m + 1$, let $H \in V(\mathcal{H})$ be a maximal element with respect to $\prec$. Let $\mathcal{G}_r = \mathcal{G} \backslash H$. Since H is a maximal element, a restricted system of the $\mathcal{G}_r$-subsystem is also a restricted system of (2). Since $|V(\mathcal{G}_r)/\sim| = m$, by our induction assumption we know the $\mathcal{G}_r$ subsystem has a nonnegative equilibrium u_r^* that attracts all positive solutions. Now the asymptotic behaviours of H subsystem are the same as those of the limiting system, the restricted system on H at $c = (u_r^*, 0)$, by the theory of asymptotically autonomous systems [12]. By assumption (A_3), the H-subsystem has a nonnegative equilibrium u_H^* that attracts positive solutions. Therefore system (2) has a nonnegative equilibrium $u^* = (u_r^*, u_H^*)$ that attracts all positive solutions of (2). □

System (2) may have multiple mixed equilibria which stay on the boundary of the phase space. A globally attracting equilibrium can only be expected to attract all positive solutions and such an equilibrium is necessarily unique. It is possible that system (2) does not have any positive equilibrium. In this case, the global attracting equilibrium in Theorem 2.3 is of a mixed type. In the rest of the section, we investigate the characteristics of the global attracting equilibrium.

Let $\mathcal{P}$ denote the set of all nonnegative equilibria of (2). We have the following result.

Theorem 2.4. Assume that assumptions (A_1) and (A_2) are satisfied. For $u^* \in \mathcal{P}$, the following statements hold.

(a) If an arc from j to i exists, then $Pu_j^* > 0$ implies $Pu_i^* > 0$.
(b) For $i, j \in V(\mathcal{G})$ such that $j \preceq i$, $Pu_j^* > 0$ implies $Pu_i^* > 0$.
(c) Let $H \in V(\mathcal{H})$ be a strongly connected component of $\mathcal{G}$. Then for all $i \in H$, Pu_i^* are either all zero or all positive.

Proof. By assumption (A_2), $Pu_j^* > 0$ implies $Pg_{ij}(u_i^*, Pu_j^*) \neq 0$. Therefore, there exists a coupling entry m such that $g_{ij}^m(u_i^*, Pu_j^*) > 0$. Assume that $Pu_i^* = 0$, by assumption (A_1), $Pf_i(u_i) \geq 0$. Then $(u_i^m)'|_{u^*} = f_i^m(u^*) + \sum_{k=1}^n g_{ik}^m(u^*, Pu_k^*) \geq g_{ij}^m(u_i^*, Pu_j^*) > 0$. This contradicts the fact that u^* is an equilibrium. Thus $Pu_i^* \neq 0$. By assumption (A_1), for $\forall i$, either $Pu_i^* > 0$ or $Pu_i^* = 0$. Therefore $Pu_i^* > 0$.

For (b), if $j \preceq i$, then there is a directed path from j to i. Let the path be $(j, j_1 \ldots, j_k, i)$. Using (a) repeatedly, $Pu_j^* > 0$ implies $Pu_i^* > 0$.

For (c), if vertices i and j are in the same strongly connected components, then $i \preceq j$ and $j \preceq i$. By (b), we get $Pu_i^* > 0 \Leftrightarrow Pu_j^* > 0$. □

For the restricted system (5) with $H \in V(\mathcal{H})$, $c \geq 0$, we have the following result.

Proposition 2.5. *Let u^{**} be an equilibrium of the restricted system (5). Then Pu_i^{**} are either positive for all $i \in H$ or zero for all $i \in H$. Furthermore, if there exists l such that $c_l > 0$, then $Pu_i^{**} > 0$ for all $i \in H$.*

Proof. Using a similar argument as in the proof of Theorem 2.4, the signs of Pu_i^{**} are the same since there is only one strongly connected component in system (5). If there exist l such that $c_l > 0$, then $g_{kl}(u_i, Pc_l) \neq 0$ for some k. This implies that $Pu_k^{**} > 0$, and thus $Pu_i^{**} > 0$ for all $i \in H$. $\quad\square$

We define a mapping $\pi : \mathcal{P} \to (0, 1)^{|V(\mathcal{H})|}$ by

$$\pi : u^* \mapsto \tilde{u}^* = (\tilde{u}_H^*)_{H \in V(\mathcal{H})}, \tag{6}$$

and

$$\tilde{u}_H^* = \begin{cases} 0 & \text{if } Pu_i^* = 0, \text{ for } i \in H, \\ 1 & \text{if } Pu_i^* > 0, \text{ for } i \in H, \end{cases}$$

where $|V(\mathcal{H})|$ is the order of set $V(\mathcal{H})$. From Theorem 2.4, we can see that mapping π is well defined and has the following property.

Proposition 2.6. *For $u^* \in \mathcal{P}$, if $H \prec H'$, then $\tilde{u}_H^* \leq \tilde{u}_{H'}^*$.*

The following result follows from Proposition 2.6.

Proposition 2.7. *An equilibrium $u^* \in \mathcal{P}$ is positive if and only if $\tilde{u}_H^* = 1$ at all minimal elements $H \in V(\mathcal{H})$.*

Proposition 2.8. *Suppose that assumptions (A_3) and (A_4) are satisfied. Then*

(a) *For $H \in V(\mathcal{H})$ and $c \geq 0$, the positive or boundary equilibrium of restricted system (5) on H at c is unique.*
(b) *The mapping π is one-to-one.*

Proof. When assumption (A_3) is satisfied, the positive equilibrium of system (5) is automatically unique, since otherwise the globally stable equilibrium cannot attract orbits originated from the other positive equilibria. If $c \neq 0$, then, By Proposition 2.5, system (5) only has positive equilibrium which is automatically unique. If $c = 0$ then system (5) breaks into independent systems $u_i' = f_i(u_i)$, $i \in H$. Assumption (A_4) guarantees the boundary equilibrium of system (5) is unique.

To see that π is one-to-one, suppose that $\pi(P^*) = \pi(P^{**})$ for $P^*, P^{**} \in \mathcal{P}$. We use induction on the order $|V(\mathcal{H})|$ of $V(\mathcal{H})$. Suppose that the claim holds for $|\mathcal{H}| = m$. Then, when $|V(\mathcal{H})| = m + 1$, we can identify a maximal element H in the ordered set $(V(\mathcal{H}), \prec)$. Let $\mathcal{G}_c = \mathcal{G} \setminus H$, then variables in H will not appear in $V(\mathcal{G}_c)$ subsystem. Let $V(\mathcal{H}_c) = V(\mathcal{G}_c)/\sim = V(\mathcal{H}) \setminus H$. Then $\mathcal{H}_c$ is a subgraph of $\mathcal{H}$ with $|V(\mathcal{H}_c)| = m$, and $P_{H'}^* = P_{H'}^{**}$, for $H' \in V(\mathcal{H}_c)$. Therefore, by our induction hypothesis,

$$P^*|_{\mathcal{G}_c} = P^{**}|_{\mathcal{G}_c}.$$

Furthermore, $P^*|_H$ and $P^{**}|_H$ are the equilibrium of the restricted system on H at $c = (P^*|_{\mathcal{G}_c}, 0)$. By (a), $\tilde{P}_H^* = \tilde{P}_H^{**}$ implies $P^* = P^{**}$ on H since the boundary or positive equilibrium is unique for system (5). Therefore, $P^* = P^{**}$ over the entire graph $\mathcal{G}$, and the claim holds for $|\mathcal{H}| = m + 1$. $\quad\square$

Define an evaluation function $E : \mathcal{P} \to \mathbb{R}_+$ as $E(u^*) = \sum_{H \in V(\mathcal{H})} \pi(u^*)_H$ for $u^* \in \mathcal{P}$. The following results identify the global attracting equilibrium.

Theorem 2.9. *Suppose that (A_3) and (A_5) are satisfied. Then the following holds.*

(a) *All positive solutions of system (2) converge to a maximizer of function E.*
(b) *If in addition (A_4) is satisfied, then the maximizer of function E is unique.*

Proof. To show (a), we note that since function E takes only integer values and is bounded by $|V(\mathcal{H})|$, a maximizer exists. Let u^* be a maximizer of function E. For any u^{**} that does not maximize function E, let $H \in V(\mathcal{H})$ be the minimal component such that $\tilde{u}_H^* > \tilde{u}_H^{**}$. Then $\tilde{u}_H^* = 1$, $\tilde{u}_H^{**} = 0$. By Proposition 2.6, for $H' \prec H$, $\tilde{u}_{H'}^* = \tilde{u}_{H'}^{**} = 0$. Therefore the limiting system of H-subsystem is the same as H-reduced subsystem. Since $\tilde{u}_H^* = 1$, the reduced H-subsystem has a positive equilibrium. By assumption (A_5), the reduced H-subsystem is persistent, and thus the coordinates of a positive solution $x(t)$ in component H will not converge to boundary equilibrium $u^{**}|_H$. Therefore solutions in the interior of region $\mathbb{R}_+^d$ will not converge to u^{**}.

To show the uniqueness of the maximizer, we assume the opposite. Let u^*, u^{**} be two minimizers and $u^* \neq u^{**}$. By assumption (A_4), the mapping π is one to one, and thus $\pi(u^*) \neq \pi(u^{**})$. There exists a minimal element $H \in V(\mathcal{H})$ such that $u^{**}_H > u^*_H$. Thus $u^{**}_H = 1$, $\tilde{u}^*_H = 0$. Using a similar argument as in the proof of (a), we know the solution in the interior of $\mathbb{R}_+^d \times \cdots \times \mathbb{R}_+^d$ will not converge to u^*. Then the solution in the interior will not converge to any maximizers of E, contradicting (a). Therefore the maximizer of function E is unique. $\quad\square$

3. A general class of multi-group epidemic models

We consider the following system of multi-group epidemic models of SEIR type:

$$\begin{aligned} S_i' &= \Lambda_i - d_i^S S_i - \sum_{j=1}^n \beta_{ij} f_{ij}(S_i, I_j), \\ E_i' &= \sum_{j=1}^n \beta_{ij} f_{ij}(S_i, I_j) - (d_i^E + \epsilon_i) E_i, \qquad i = 1, \ldots, n, \\ I_i' &= \epsilon_i E_i - (d_i^I + \gamma_i) I_i, \end{aligned} \tag{7}$$

where S_i, E_i, and I_i denote the number of individuals in the susceptible, exposed, and infectious compartments in the ith group of the host population, respectively. The number of individuals in the recovered compartment of the ith group is denoted by R_i, and R_i satisfies the following equation:

$$R_i' = \epsilon_i E_i - d_i^R R_i. \tag{8}$$

Since equations in (7) do not contain variable R_i, we will first establish the global dynamics of system (7), and then derive the asymptotic behaviours of R_i from Eq. (8).

All parameters in system (7)–(8) are assumed to be nonnegative. We further assume that $d_k^S, d_k^E, d_k^I, d_k^R, \Lambda_k > 0$ for all k. For $i \neq j$, the incidence term $\beta_{ij} f_{ij}(S_i, I_j)$ describes the cross-infection from group j to group i. Motivated by biological considerations, we assume that $f_{ij}(0, I_j) = 0$, $f_{ij}(S_i, 0) = 0$, and $f_{ij}(S_i, I_j) > 0$ for $S_i > 0$, $I_j > 0$. We also assume that $f_{ij}(S_i, I_j)$ are sufficiently smooth.

For each i, adding the three equations in (3) gives

$$(S_i + E_i + I_i)' \leq \Lambda_i - d_i^*(S_i + E_i + I_i)$$

with $d_i^* = \min\{d_i^S, d_i^E, d_i^I + \gamma_i\} > 0$. Hence $\limsup_{t \to \infty}(S_i + E_i + I_i) \leq \Lambda_i/d_i^*$. Similarly, from the S_i equation we obtain $\limsup_{t \to \infty}$

$S_i \leq \Lambda_i/d_i^S$. Therefore, omega limit sets of system (3) are contained in the following bounded region in the nonnegative orthant of $\mathbb{R}^{3n}$

$$\Gamma = \left\{ (S_1, E_1, I_1, \ldots, S_n, E_n, I_n) \in \mathbb{R}_+^{3n} \mid 0 < S_i \leq \frac{\Lambda_i}{d_i^S}, \right.$$
$$\left. S_i + E_i + I_i \leq \frac{\Lambda_i}{d_i^*}, \text{ for all } i \right\}.$$

It can be verified that region Γ is positively invariant.

System (3) always has the *disease-free equilibrium* $P_0 = (S_1^0, 0, 0, \ldots, S_n^0, 0, 0)$, on the boundary of Γ, where $S_i^0 = \Lambda_i/d_i^S$. An equilibrium $P^* = (S_1^*, E_1^*, I_1^*, \ldots, S_n^*, E_n^*, I_n^*)$ is called an *endemic equilibrium* of (3) if $E_i^*, I_i^* > 0$ for all $i = 1, \ldots, n$, and P^* is called a *mixed equilibrium* if $E_i^*, I_i^* > 0$ for some $1 \leq i \leq n$ while $E_i^* = I_i^* = 0$ for other i. We can see that mixed equilibria are necessarily on the boundary of Γ, and an endemic equilibrium belongs to the interior of Γ.

We further make the following assumptions on the incidence function $f_{ij}(S_i, I_j)$:

(F$_1$) $0 < \lim_{I_j \to 0^+} \frac{f_{ij}(S_i, I_j)}{I_j} = C_{ij}(S_i) \leq +\infty$, $0 < S_i \leq S_i^0$.

(F$_2$) $f_{ij}(S_i, I_j) \leq C_{ij}(S_i)I_j$ for all $I_j > 0$.

(F$_3$) $C_{ij}(S_i) \leq C_{ij}(S_i^0)$, $0 < S_i < S_i^0$.

If a positive equilibrium $P^* = (S^*, E^*, I^*)$ of (7) exists, we assume that

(F$_4$) $(S_i - S_i^*)(f_{ii}(S_i, I_i^*) - f_{ii}(S_i^*, I_i^*)) > 0$, $S_i \neq S_i^*$.

(F$_5$) $[f_{ij}(S_i, I_j)f_{ii}(S_i^*, I_i^*) - f_{ij}(S_i^*, I_j^*)f_{ii}(S_i, I_i^*)]\left[\frac{f_{ij}(S_i, I_j)f_{ii}(S_i^*, I_i^*)}{I_j}\right.$
$\left. - \frac{f_{ij}(S_i^*, I_j^*)f_{ii}(S_i, I_i^*)}{I_j^*}\right] \leq 0$, $S_i, I_j > 0$.

Classes of $f_{ij}(S_i, I_j)$ satisfying (F$_1$)–(F$_3$) include common incidence functions such as bilinear incidence $f_{ij}(S_i, I_j) = I_j S_i$, nonlinear incidence $f_{ij}(S_i, I_j) = I_j^{p_j} S_i^{q_i}$, and saturated incidences $f_{ij}(S_i, I_j) = \frac{I_j^{p_j}}{I_j + A_j} \frac{S_i^{q_i}}{S_i + B_i}$. For detailed description of the model, we refer the reader to [1,11,2].

The basic reproduction number R_0 for an epidemic model measures the average number of secondary infections caused by a single infectious individual in an entirely susceptible population during its infectious period. Assume that $f_{ij}(S_i, I_j)$ satisfies (F$_1$), and let

$$M_0 = M(S_1^0, S_2^0, \ldots, S_n^0) = \left(\frac{\beta_{ij}\epsilon_i C_{ij}(S_i^0)}{(d_i^E + \epsilon_i)(d_i^I + \gamma_i)} \right)_{1 \leq i,j \leq n}. \tag{9}$$

It can be shown using the method of next generation matrix as in [13] that R_0 for system (3) is

$$R_0 = \rho(M_0), \tag{10}$$

where ρ is the spectral radius of the matrix. If $C_{ij}(S_i^0) = +\infty$ for some i and j, it is understood that $R_0 = +\infty$, see also [1].

System (7) is an example of coupled system on networks (2). The vertex system is a single-group SEIR model with vector field

$$f_i = (\Lambda_i - d_i^S S_i, -(d_i^E + \epsilon_i)E_i, \epsilon_i E_i - (d_i^I + \gamma_i)I_i).$$

The group-contact network is defined by the digraph $(\mathcal{G}, B)$, weighted by the transmission matrix $B = \{\beta_{ij}\} \geq 0$. A directed arc from vertex j to i exists if and only if $\beta_{ij} > 0$. The general coupling terms are given by $g_{ij} = (-\beta_{ij}f_{ij}, \beta_{ij}f_{ij}, 0)$, and they represents cross-infections among groups. Let $u_i = (S_i, E_i, I_i)^T$ be the state variable and the projection matrix

$$P = \begin{pmatrix} 0 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{pmatrix}.$$

Then the coupling variables are $Pu_i = (E_i, I_i)^T$. At an equilibrium $u^* = (u_1^*, \ldots, u_n^*)$ with $u_i^* = (S_i^*, E_i^*, I_i^*)$, $Pu_i^* > 0$ if and only if $E_i^* > 0$ and $I_i^* > 0$, namely the disease is endemic in the group i, and $Pu_i^* = 0$ if and only if $E_i^* = I_i^* = 0$, namely, the group i is disease free.

Under the assumption that the transmission matrix $B = \{\beta_{ij}\}$ is irreducible, or equivalently, the digraph $(\mathcal{G}, B)$ is strongly connected, the following threshold result is established in [1]. A similar result for an n-group SIR model was first established in [11].

Theorem 3.1 (*Li and Shuai*). *Assume that $B = (\beta_{ij})$ is irreducible.*

(a) *If $R_0 \leq 1$, then P_0 is the only equilibrium which is globally asymptotically stable in Γ.*

(b) *If $R_0 > 1$, then system (7) has a unique endemic equilibrium P^*, and P^* is globally asymptotically stable in the interior of Γ if assumptions (F$_4$) and (F$_5$) are satisfied.*

When the irreducibility assumption on the transmission matrix $B = (\beta_{ij})$ is dropped, the digraph $(\mathcal{G}, B)$ is no longer strongly connected. We show in the following that all groups within a strongly connected component H have the same behaviours. From the form of functions $f_i(u_i)$ and $g_{ij}(u_i, u_j)$, we can verify that conditions in (A$_1$) and (A$_2$) are satisfied. From Theorem 2.4 we have the following result.

Proposition 3.2. *Let $u^* = (S_i^*, E_i^*, I_i^*)_{i \in V(\mathcal{G})}$ be an equilibrium and H be a strongly connected component of $(\mathcal{G}, B)$. Either $E_i^* = I_i^* = 0$ for all $i \in H$ or $E_i^* > 0$, $I_i^* > 0$ for all $i \in H$.*

The condensed graph $\mathcal{H}$, sub-systems, reduced sub-systems, restricted systems and the set of equilibria $\mathcal{P}$ can be defined for $(\mathcal{G}, B)$ and system (7) in the same way as in Section 2. For a strongly connected component $H \in V(\mathcal{H})$, the reduced H-subsystem is a closed system. Let $R_{0,H}$ denote its basic reproduction number. Since the reduced H-subsystem has an irreducible transmission matrix, it satisfies Theorem 3.1. Therefore, if $R_{0,H} \leq 1$ all solutions of the reduced H-subsystem converge to the disease-free equilibrium, and if $R_{0,H} > 1$, all solutions of reduced H-subsystem converge to a unique endemic equilibrium.

The following result establishes the relation between the basic reproduction number R_0 for the entire system and $R_{0,H}$.

Theorem 3.3. *Let $\mathcal{H}$ be the condensing graph of $(\mathcal{G}, B)$. Then*

$$R_0 = \max\{R_{0,H} \mid H \in V(\mathcal{H})\}. \tag{11}$$

Proof. Theorem 3.3 holds trivially if B is irreducible. Suppose that B is reducible. For a strongly connected component $H \in V(\mathcal{H})$, let

$$M_{0,H} = \left(\frac{\beta_{ij}\epsilon_i C_{ij}(S_i^0)}{(d_i^E + \epsilon_i)(d_i^I + \gamma_i)} \right)_{i,j \in V(H)}.$$

Then $R_{0,H} = \rho(M_{0,H})$. If we group the equations in (7) according to strongly connected components of $(\mathcal{G}, B)$ and rearrange the components according to the order $\prec$ defined on $\mathcal{H}$, then matrix M_0 in (9) can be written in block-triangular form

$$M_0 = \begin{bmatrix} M_{0,H_1} & 0 & \cdots & 0 \\ * & M_{0,H_2} & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ * & * & \cdots & M_{0,H_N} \end{bmatrix},$$

where $H_1, \ldots, H_N$ are the vertices of the condensed graph $\mathcal{H}$. Using Cauchy–Binet formula we see that eigenvalues of M_0 are the ensemble of eigenvalues of M_{0,H_i}, $i = 1, \ldots, N$. This leads to relation (11). $\square$

From Theorem 3.3 we see that network connectivity has a strong impact on the endemicity of disease transmission. When the group-contact network is not strongly connected, the basic reproduction number $R_0 > 1$ only implies that $R_{0,H} > 1$ on some components H. As a result, the disease may be endemic in some groups and disappears from other groups. It is possible that an endemic equilibrium may not exist, and that system (7) can have multiple mixed equilibria. It is of interest to investigate whether $R_0 > 1$ can imply the existence of a positive endemic equilibrium, and whether global convergence to an equilibrium still holds. Suppose that $R_0 > 1$ and no positive equilibrium exists, it is then of interest to investigate which of the many mixed equilibria will be globally stable. The theory developed in Section 2 will be applied to investigate the global dynamics of system (7) and address these issues.

Each vertex system is a single-group SEIR model and has a unique boundary equilibrium $(S_i, 0, 0)$, and thus assumption (A_4) is satisfied. For any strongly connected component H, global dynamics of the reduced H-subsystem satisfy Theorem 3.1. In particular, when a positive equilibrium exists, we know $R_{0,H} > 1$ and a unique endemic equilibrium for the reduced system exists and is globally stable. Thus assumption (A_5) is also satisfied.

Next we show that system (7) satisfies assumption (A_3). Let $H \in V(\mathcal{H})$ be a strongly connected component and $c \geq 0$. The restricted subsystem on H at c is:

$$S_i' = \Lambda_i - d_i^S S_i - \sum_{j \in H} \beta_{ij} f_{ij}(S_i, I_j) - \sum_{j \in V(\mathcal{G}) \setminus H} \beta_{ij} f_{ij}(S_i, c_j)$$

$$E_i' = \sum_{j \in H} \beta_{ij} f_{ij}(S_i, I_j) + \sum_{j \in V(\mathcal{G}) \setminus H} \beta_{ij} f_{ij}(S_i, c_j) \qquad (12)$$

$$\qquad - (d_i^E + \epsilon_i) E_i, \quad i \in H$$

$$I_i' = \epsilon_i E_i - (d_i^I + \gamma_i) I_i.$$

We want to show that system (12) has a unique positive equilibrium that attracts all positive solutions. We will establish the result for a more general system:

$$S_i' = \Lambda_i - d_i^S S_i - \sum_{j=1}^n \beta_{ij} f_{ij}(S_i, I_j) - h_i(S_i, I_i),$$

$$E_i' = \sum_{j=1}^n \beta_{ij} f_{ij}(S_i, I_j) + p_i h_i(S_i, I_i) - (d_i^E + \epsilon_i) E_i, \qquad (13)$$

$$\qquad i = 1, 2, \ldots, n,$$

$$I_i' = \epsilon_i E_i + q_i h_i(S_i, I_i) - (d_i^I + \gamma_i) I_i,$$

where p_i, q_i satisfy $p_i, q_i \geq 0$ and $0 < p_i + q_i \leq 1$ for all i, $h_i(S_i, I_i) \geq 0$. Other parameters have the same interpretation as in system (7). Let $B = \{\beta_{ij}\}$ and $(\mathcal{G}, B)$ to represent the weighted digraph corresponding to B.

System (13) can be regarded as a general multi-group model with vertical transmission: functions $h_i(S_i, I_i)$ can be understood as newborns infected at birth in the ith group, and enter compartments E_i and I_i by fractions p_i and q_i respectively. It can be verified that the feasible region for system (13) is

$$\Delta = \left\{ (S_1, E_1, I_1, \ldots, S_n, E_n, I_n) \in \mathbb{R}_+^{3n} \mid 0 < S_i \leq \frac{\Lambda_i}{d_i^S}, \right.$$

$$\left. S_i + E_i + I_i \leq \frac{\Lambda_i}{d_i^*}, \text{ for all } i \right\},$$

with $d_i^* = \min\{d_i^S, d_i^E, d_i^I\}$. An equilibrium $P^* = (S_1^*, E_1^*, I_1^*, \ldots, S_n^*, E_n^*, I_n^*)$ of system (13) satisfies the following equilibrium equations

$$0 = \Lambda_i - d_i^S S_i^* - \sum_{j=1}^n \beta_{ij} f_{ij}(S_i^*, I_j^*) - h_i(S_i^*, I_i^*),$$

$$0 = \sum_{j=1}^n \beta_{ij} f_{ij}(S_i^*, I_j^*) + p_i h_i(S_i^*, I_i^*) - (d_i^E + \epsilon_i) E_i^*, \qquad (14)$$

$$\qquad i = 1, 2, \ldots, n.$$

$$0 = \epsilon_i E_i^* + q_i h_i(S_i^*, I_i^*) - (d_i^I + \gamma_i) I_i^*.$$

Proposition 3.4. *Assume that $B = \{\beta_{ij}\}$ is irreducible and there exists k such that $h_k(S_k, I_k) > 0$ in Δ. Then*

(a) *system (13) has no equilibria on the boundary of Δ, and*
(b) *system (13) has an endemic (positive) equilibrium.*

Proof. By the positive invariance of the compact and convex feasible region Δ and Browder's Fixed Point Theorem [14], we can deduce that system (13) has an equilibrium in Δ. Let $P^* = (S_1^*, E_1^*, I_1^*, \ldots, S_n^*, E_n^*, I_n^*)$ be an equilibrium of system (13). From the first equation of (14) we get $S_i^* > 0$ for all i since $f_{ij}(0, I_j) = 0$.

Suppose $h_k > 0$ for some k. Then from (14),

$$(d_k^E + \epsilon_k) E_k^* = \sum_{j=1}^n \beta_{kj} f_{ij}(S_k^*, I_j^*) + p_k h_k(S_k^*, I_k^*),$$

$$(d_k^I + \gamma) I_k^* = \epsilon_k E_k^* + q_k h_k(S_k^*, I_k^*).$$

Therefore, $h_k(S_k^*, I_k^*) > 0$ implies that $Pu_k^* = (E_k^*, I_k^*)^T > 0$. Since $(\mathcal{G}, B)$ is strongly connected, we know $Pu_i^* > 0$ for all i, and system (13) has an endemic equilibrium and no boundary equilibria. □

Let $P^* = (S_1^*, E_1^*, I_1^*, \ldots, S_n^*, E_n^*, I_n^*)$ be an endemic equilibrium of (13). We make the following assumption on $h_i(S_i, I_i)$:

(F_6) $\left(1 - \frac{I_i f_{ii}(S_i, I_i^*) h_i(S_i^*, I_i^*)}{I_i^* f_{ii}(S_i^*, I_i^*) h_i(S_i, I_i)}\right) \left(\frac{f_{ii}(S_i^*, I_i^*) h_i(S_i, I_i)}{f_{ii}(S_i, I_i) h_i(S_i^*, I_i^*)} - 1\right) \leq 0$, for all $S_i, I_i > 0$.

The next result establishes the global dynamics of system (13) when B is irreducible. It generalizes the global stability result in [1,11].

Theorem 3.5. *Suppose that $B = \{\beta_{ij}\}$ is irreducible and there exists k such that $h_k(S_k, I_k) > 0$ in Δ. Assume that (F_4), (F_5) and (F_6) hold. Then system (13) has a unique endemic equilibrium and it is globally asymptotically stable with respect to the interior of Δ.*

Proof. Let $P^* = (S_1^*, E_1^*, I_1^*, \ldots, S_n^*, E_n^*, I_n^*)$ be an endemic equilibrium of (13). Consider a Lyapunov function of form $V = \sum_{i=1}^n c_i V_i$, where c_i is the cofactor of the ith diagonal entry of the algebraic Laplacian matrix of B, as defined in [1], and

$$V_i = \int_{S_i^*}^{S_i} \frac{f_{ii}(\xi, I_i^*) - f_{ii}(S_i^*, I_i^*)}{f_{ii}(\xi, I_i^*)} d\xi + E_i$$

$$\qquad - E_i^* \log E_i + \frac{d_i^E + \epsilon_i}{\epsilon_i} (I_i - I_i^* \log I_i).$$

Taking the derivative of V_i along solutions to system (13), we obtain

$$\dot{V}_i = \left(1 - \frac{f_{ii}(S_i^*, I_i^*)}{f_{ii}(S_i, I_i^*)}\right) \left(\Lambda_i - d_i^S S_i - \sum_{j=1}^n \beta_{ij} f_{ij}(S_i, I_j) - h_i(S_i, I_i)\right)$$

$$\qquad + \sum_{j=1}^n \beta_{ij} f_{ij}(S_i, I_j) + p_i h_i(S_i, I_i) - (d_i^E + \epsilon_i) E_i$$

$$\qquad - \frac{E_i^*}{E_i} \sum_{j=1}^n \beta_{ij} f_{ij}(S_i, I_j) - \frac{E_i^*}{E_i} p_i h_i(S_i, I_i) + (d_i^E + \epsilon_i) E_i^*$$

$$+ (d_i^E + \epsilon_i)E_i - \frac{(d_i^E + \epsilon_i)(d_i^I + \gamma_i)}{\epsilon_i}I_i + \frac{(d_i^E + \epsilon_i)}{\epsilon_i}q_i h_i(S_i, I_i)$$

$$- \frac{I_i^*}{I_i}(d_i^E + \epsilon_i)E_i + \frac{(d_i^E + \epsilon_i)(d_i^I + \gamma_i)}{\epsilon_i}I_i^*$$

$$- \frac{(d_i^E + \epsilon_i)I^*}{\epsilon_i I}q_i h_i(S_i, I_i)$$

$$\leq -d_i^S\left(S_i - S_i^*\right)\left(1 - \frac{f_{ii}(S_i^*, I_i^*)}{f_{ii}(S_i, I_i^*)}\right)$$

$$+ \sum_{j=1}^{n}\beta_{ij}f_{ij}(S_i^*, I_j^*)\left[3 + \frac{f_{ii}(S_i^*, I_i^*)f_{ij}(S_i, I_j)}{f_{ii}(S_i, I_i^*)f_{ij}(S_i^*, I_j^*)} - \frac{f_{ii}(S_i^*, I_i^*)}{f_{ii}(S_i, I_i^*)}\right.$$

$$\left. - \frac{E_i^* f_{ij}(S_i, I_j)}{E_i f_{ij}(S_i^*, I_j^*)} - \frac{I_i}{I_i^*} - \frac{E_i I_i^*}{E_i^* I_i}\right]$$

$$+ p_i h_i(S_i^*, I_i^*)\left[3 + \frac{f_{ii}(S_i^*, I_i^*)h_i(S_i, I_i)}{f_{ii}(S_i, I_i^*)h_i(S_i^*, I_i^*)} - \frac{f_{ii}(S_i^*, I_i^*)}{f_{ii}(S_i, I_i^*)}\right.$$

$$\left. - \frac{E_i^* h_i(S_i, I_i)}{E_i h_i(S_i^*, I_i^*)} - \frac{I_i}{I_i^*} - \frac{E_i I_i^*}{E_i^* I_i}\right]$$

$$+ q_i h_i(S_i^*, I_i^*)\left[2 + \frac{f_{ii}(S_i^*, I_i^*)h_i(S_i, I_i)}{f_{ii}(S_i, I_i^*)h_i(S_i^*, I_i^*)} - \frac{I_i^* h_i(S_i, I_i)}{I_i h_i(S_i^*, I_i^*)}\right.$$

$$\left. - \frac{I_i}{I_i^*} - \frac{f_{ii}(S_i^*, I_i^*)}{f_{ii}(S_i, I_i^*)}\right].$$

Let

$$Q_i(S_i, E_i, I_i) = 3 + \frac{f_{ii}(S_i^*, I_i^*)h_i(S_i, I_i)}{f_{ii}(S_i, I_i^*)h_i(S_i^*, I_i^*)} - \frac{f_{ii}(S_i^*, I_i^*)}{f_{ii}(S_i, I_i^*)} - \frac{E_i^* h_i(S_i, I_i)}{E_i h_i(S_i^*, I_i^*)}$$

$$- \frac{I_i}{I_i^*} - \frac{E_i I_i^*}{E_i^* I_i},$$

$$R_i(S_i, E_i, I_i) = 2 + \frac{f_{ii}(S_i^*, I_i^*)h_i(S_i, I_i)}{f_{ii}(S_i, I_i^*)h_i(S_i^*, I_i^*)} - \frac{I_i^* h_i(S_i, I_i)}{I_i h_i(S_i^*, I_i^*)}$$

$$- \frac{I_i}{I_i^*} - \frac{f_{ii}(S_i^*, I_i^*)}{f_{ii}(S_i, I_i^*)},$$

and

$$F_{ij}(S_i, E_i, I_i, I_j) = 3 + \frac{f_{ij}(S_i, I_j)f_{ii}(S_i^*, I_i^*)}{f_{ij}(S_i^*, I_j^*)f_{ii}(S_i, I_i^*)} - \frac{f_{ii}(S_i^*, I_i^*)}{f_{ii}(S_i, I_i^*)} - \frac{f_{ij}(S_i, I_j)E_i^*}{f_{ij}(S_i^*, I_j^*)E_i}$$

$$- \frac{I_i}{I_i^*} - \frac{E_i I_i^*}{E_i^* I_i}.$$

Then

$$Q_i(S_i, E_i, I_i) = \left(4 - \frac{f_{ii}(S_i^*, I_i^*)}{f_{ii}(S_i, I_i^*)} - \frac{E_i^* h_i(S_i, I_i)}{E_i h_i(S_i^*, I_i^*)}\right.$$

$$\left. - \frac{I_i f_{ii}(S_i^*, I_i^*)h_i(S_i, I_i^*)}{I_i^* f_{ii}(S_i^*, I_i^*)h_i(S_i, I_i)} - \frac{E_i I_i^*}{E_i^* I_i}\right)$$

$$+ \left(1 - \frac{I_i f_{ii}(S_i^*, I_i^*)h_i(S_i^*, I_i^*)}{I_i^* f_{ii}(S_i^*, I_i^*)h_i(S_i, I_i)}\right)\left(\frac{f_{ii}(S_i^*, I_i^*)h_i(S_i, I_i)}{f_{ii}(S_i, I_i^*)h_i(S_i^*, I_i^*)} - 1\right)$$

$$\leq \left(1 - \frac{I_i f_{ii}(S_i^*, I_i^*)h_i(S_i^*, I_i^*)}{I_i^* f_{ii}(S_i^*, I_i^*)h_i(S_i, I_i)}\right)\left(\frac{f_{ii}(S_i^*, I_i^*)h_i(S_i, I_i)}{f_{ii}(S_i, I_i^*)h_i(S_i^*, I_i^*)} - 1\right)$$

$$\leq 0,$$

by assumption (F$_6$). Similarly,

$$R_i(S_i, E_i, I_i)$$

$$= \left(3 - \frac{f_{ii}(S_i^*, I_i^*)}{f_{ii}(S_i, I_i^*)} - \frac{I_i^* h_i(S_i, I_i)}{I_i h_i(S_i^*, I_i^*)} - \frac{I_i f_{ii}(S_i^*, I_i^*)h_i(S_i^*, I_i^*)}{I_i^* f_{ii}(S_i^*, I_i^*)h_i(S_i, I_i)}\right)$$

$$+ \left(1 - \frac{I_i f_{ii}(S_i^*, I_i^*)h_i(S_i^*, I_i^*)}{I_i^* f_{ii}(S_i^*, I_i^*)h_i(S_i, I_i)}\right)\left(\frac{f_{ii}(S_i^*, I_i^*)h_i(S_i, I_i)}{f_{ii}(S_i, I_i^*)h_i(S_i^*, I_i^*)} - 1\right)$$

$$\leq \left(1 - \frac{I_i f_{ii}(S_i^*, I_i^*)h_i(S_i^*, I_i^*)}{I_i^* f_{ii}(S_i^*, I_i^*)h_i(S_i, I_i)}\right)\left(\frac{f_{ii}(S_i^*, I_i^*)h_i(S_i, I_i)}{f_{ii}(S_i, I_i^*)h_i(S_i^*, I_i^*)} - 1\right)$$

$$\leq 0.$$

Using assumption (F$_4$) we obtain

$$\dot{V}_i \leq \sum_{j=1}^{n}\beta_{ij}f_{ij}(S_i^*, I_j^*)F_{ij}(S_i, E_i, I_i, I_j).$$

Let $\Phi(a) = 1 - a + \log a$ and $L_i(I_i) = -\frac{I_i}{I_i^*} + \log\frac{I_i}{I_i^*}$. Then $\Phi(a) \leq 0$ for $a > 0$ and the equality holds only at $a = 1$. Furthermore,

$$F_{ij} = L_i(I_i) - L_j(I_j) + \Phi\left(\frac{f_{ii}(S_i^*, I_i^*)}{f_{ii}(S_i, I_i^*)}\right) + \Phi\left(\frac{E_i I_i^*}{E_i^* I_i}\right)$$

$$+ \Phi\left(\frac{I_j f_{ij}(S_i^*, I_j^*)f_{ii}(S_i^*, I_i^*)}{I_j^* f_{ij}(S_i, I_j)f_{ii}(S_i, I_i^*)}\right) + \Phi\left(\frac{f_{ij}(S_i, I_j)E_i^*}{f_{ij}(S_i^*, I_j^*)E_i}\right)$$

$$+ \left(\frac{f_{ij}(S_i, I_j)f_{ii}(S_i^*, I_i^*)}{f_{ij}(S_i^*, I_j^*)f_{ii}(S_i, I_i^*)} - 1\right)\left(1 - \frac{I_j f_{ij}(S_i^*, I_j^*)f_{ii}(S_i^*, I_i^*)}{I_j^* f_{ij}(S_i, I_j)f_{ii}(S_i, I_i^*)}\right)$$

$$\leq L_i(I_i) - L_j(I_j).$$

This shows that $\{F_{ij}\}$ satisfy the cycle condition in Corollary 3.3 of [1], and thus, the function V satisfies $\dot{V} \leq 0$ for all $(S_1, E_1, I_1, \ldots, S_n, E_n, I_n) \in \Delta$.

In any subset of $\{(S_1, E_1, I_1, \ldots, S_n, E_n, I_n) \mid \dot{V} = 0\}$ that is invariant for system (13), we necessarily have $d_i^S(S_i - S_i^*)(1 - \frac{f_{ii}(S_i^*, I_i^*)}{f_{ii}(S_i, I_i^*)}) = 0$ and $Q_i(S_i, E_i, I_i) = 0$, for all i. It can be verified that these conditions imply $S_i = S_i^*$, $E_i = E_i^*$ and $I_i = I_i^*$ for all i. Therefore the largest invariant set where $\dot{V} = 0$ is the singleton $\{P^*\}$. LaSalle's Invariance Principle [15] implies that the equilibrium P^* is globally asymptotically stable in Δ. The uniqueness of P^* follows from its global stability. □

When $(\mathcal{G}, B)$ is not strongly connected, the restricted system (12) on a strongly connected component H has its β_{ij} from the weight matrix of the subgraph H, and hence (12) is a special case of the system (13), $p_i = 1$, $q_i = 0$ and

$$h_i(S_i, I_j) = \sum_{j \in V(\mathcal{G}) \setminus H}\beta_{ij}f_{ij}(S_i, c_j). \tag{15}$$

The following results follow from Theorem 3.5. It shows that system (7) satisfies assumption (A$_3$).

Proposition 3.6. *For any $H \in V(\mathcal{H})$, let $h_i(S_i, I_j)$ be defined as in (15).*

(a) *Suppose that there exist $k \in H$ such that $h_k(S_k, I_k) > 0$ and that f_{ij} satisfies assumptions (F$_4$)–(F$_6$). Then, the restricted system (12) has a unique endemic equilibrium and it attracts all positive solutions.*

(b) *Suppose that $h_i(S_i, I_i) = 0$ for all $i \in H$ and that f_{ij} satisfies assumptions (F$_4$) and (F$_5$). If $R_{0,H} \leq 1$ then the disease-free equilibrium is globally asymptotically stable; if $R_{0,H} > 1$, then a unique endemic equilibrium exists and it attracts all positive solutions.*

We have shown that assumptions (A_1)–(A_5) are satisfied by system (7). Let evaluation function $E : \mathscr{P} \to \mathbb{R}_+$ be defined as in Theorem 2.9. Applying Theorem 2.9, we have the following result.

Theorem 3.7. *Assume that incidence functions in* (7) *satisfy assumptions* (F_1)–(F_6). *Then all positive solutions of system* (7) *converge to the unique maximizer* P^* *of function* E.

Applying Proposition 2.7 to system (7), we can check if the globally stable equilibrium is a positive equilibrium or a mixed equilibrium.

Theorem 3.8. *Let* P^* *be the nonnegative globally asymptotically stable equilibrium of system* (7). *Then* P^* *is a positive equilibrium if and only if* $R_{0,H} > 1$ *for all minimal elements* $H \in V(\mathscr{H})$.

Corollary 3.9. *A positive equilibrium* P^* *exists if and only if* $R_{0,H} > 1$ *for all minimal elements* $H \in V(\mathscr{H})$. *In this case,* P^* *is unique and attracts all positive solutions.*

For the class of multi-group epidemic models whose incidence functions satisfy assumptions (A_1)–(A_5), Theorems 3.1, 3.3, 3.5, 3.7, 3.8 and Propositions 3.2, 3.4, 3.6 completely characterize the effects of the connectivity of the group-contact network on the endemicity of the disease. If the network is strongly connected, then the disease outcomes are completely determined by the basic reproduction number R_0 (Theorem 3.1): if $R_0 \leq 1$ the disease dies out; if $R_0 > 1$ the disease persists in all groups and all persistent solutions converge to a unique positive endemic equilibrium. If the network is not strongly connected, then R_0 no longer determines the disease outcomes. While $R_0 \leq 1$ still implies that the disease dies out from all groups, $R_0 > 1$ cannot guarantee that the disease is persistent in all groups. A positive endemic equilibrium may not exist in this case, and multiple mixed equilibria may exist depending on the network connectivity. As we show in Theorems 3.7 and 3.8 that it is productive to partition the network $(\mathscr{G}, B)$ into strongly connected components and examine the resulting condensed graph $\mathscr{H}$. A natural order $\prec$ and an evaluation function E can be defined on the set of equilibria using the induced network structure on the condensed graph $\mathscr{H}$. The unique maximizer of function E identifies the equilibrium that attracts all positive solutions. The maximizer identifies the groups in which the disease is endemic and groups in which the disease disappears. The order $\prec$ also enables us to identify minimal components in the network, whose importance in determining whether the disease is endemic in all of the groups is clearly shown in Theorem 3.8 and Corollary 3.9.

4. A spatial ecological model

We consider the following single-species ecological model with dispersal:

$$x_i' = x_i f_i(x_i) + \sum_{j=1}^{n} d_{ij}(x_j - \alpha_{ij} x_i), \quad i = 1, 2, \ldots, n. \quad (16)$$

Here $x_i \in \mathbb{R}_+$ represents density of the species on patch i. Function $f_i \in C^1(\mathbb{R}_+, \mathbb{R})$ describes the density-dependent growth rate of the species on patch i. We assume that f_i satisfies the following property: there exists constant $b_i > 0$ such that $f_i'(x_i) \leq -b_i < 0, x_i > 0$, and $f_i(0) > 0$ for $i = 1, 2, \ldots, n$. Such property is satisfied by $f_i(x_i) = r_i(1 - x_i/K_i)$ so that $x_i f_i(x_i)$ gives the logistic growth. Constants d_{ij} are the dispersal rates for the species from patch j to patch i. A detailed description of system (16) can be found in [1,16].

Let $D = (d_{ij})$ be the dispersal matrix. Consider

$$L(D) = \begin{pmatrix} -\sum_{j=1}^{n} d_{1j}\alpha_{1j} & d_{12} & \cdots & d_{1n} \\ d_{21} & -\sum_{j=1}^{n} d_{2j}\alpha_{2j} & \cdots & d2n \\ \vdots & \vdots & \ddots & \vdots \\ d_{n1} & d_{n2} & \cdots & -\sum_{j=1}^{n} d_{nj}\alpha_{nj} \end{pmatrix}$$

and the Jacobian matrix of system (16) at the equilibrium $(0, \ldots, 0)$

$$A_f = \text{diag}(f_1(0), f_2(0), \ldots, f_n(0)) + L(D). \quad (17)$$

The stability modulus of A_f is

$$s(A_f) = \max\{\text{Re } \lambda \mid \lambda \text{ is an eigenvalue of } A_f\}. \quad (18)$$

It is of interest to investigate the impact of connectivity of the dispersal network on the extinction and persistence of the species on all patches. When the dispersal matrix D is irreducible, the following threshold result is known, see [1,16].

Theorem 4.1. *Suppose that the dispersal matrix* $D = (d_{ij})$ *is irreducible. Then*

(1) *If* $s(A_f) \leq 0$, *then the extinction equilibrium* $(0, \ldots, 0)$ *is the only equilibrium of system* (16) *and is globally asymptotically stable in* $\mathbb{R}_+^n$, *and the species becomes extinct in all patches,*

(2) *If* $s(A_f) > 0$, *then the extinction equilibrium* $(0, \ldots, 0)$ *is unstable and a unique positive equilibrium* E^* *exists and is globally asymptotically stable in the interior of* $\mathbb{R}_+^n$. *The species persists in all patches.*

When the dispersal matrix D is reducible, the dispersal network $(\mathscr{G}, D)$ is not strongly connected. The species may become extinct on some patches while persists on others. It can be verified that system (16) satisfies assumptions (A_1) and (A_2). The following result follows from Theorem 2.4.

Proposition 4.2. *Let* H *be a strongly connected component of the dispersal network* $(\mathscr{G}, D)$. *Then, at an equilibrium* $x^* = (x_1^*, \ldots, x_n^*)$, *either* $x_i^* = 0$ *for all* $i \in H$ *or* $x_i^* > 0$ *for all* $i \in H$.

Proposition 4.2 implies that, at an equilibrium, on all patches in a strongly connected component, the species has the same behaviours in terms of extinction and persistence. It is natural to partition the graph into strongly connected components and consider the induced network structure on the condensed graph $\mathscr{H}$. For $H \in V(\mathscr{H})$, let $A_{f,H}$ denote the matrix A_f defined in (17) for the reduced H subsystem. The following result gives the relation of $s(A_f)$ and $s(A_{f,H})$ and can be proved as Theorem 3.3 in Section 3.

Theorem 4.3. *Let* $\mathscr{H}$ *be the condensing graph of* $(\mathscr{G}, D)$. *Then*

$$s(A_f) = \max\{s(A_{f,H}) \mid H \in V(\mathscr{H})\}. \quad (19)$$

When the dispersal matrix is reducible, by Theorem 4.3, we see that $s(A_f) > 0$ can no longer ensure the existence of a positive persistence equilibrium, and mixed equilibria may exist at which the species is extinct on some patches and persists among others. We follow the general theory developed in Section 2 to investigate the global dynamics of system (16) in this case.

Verification of assumptions (A_1), (A_2), and (A_4) is straightforward. Assumption (A_5) can be verified by applying Theorem 4.1

to the reduced H subsystem on a strongly connected component. Next we show that system (16) satisfies assumption (A$_3$).

Let $q_i = \sum_{j=1}^{n} d_{ij}\alpha_{ij}x_i \geq 0$. Then the restricted system on $H \in V(\mathcal{H})$ at c can be written as:

$$x'_i = x_i f_i(x_i) - q_i x_i + \sum_{j \in H} d_{ij}x_j + \sum_{l \in V(\mathcal{G})\backslash H} d_{il}c_l, \quad i \in H. \tag{20}$$

We consider a slightly more general system

$$x'_i = x_i f_i(x_i) - q_i x_i + \sum_{j=1}^{m} d_{ij}x_j + p_i, \quad i = 1, 2, \ldots, m, \tag{21}$$

where $p_i \geq 0$. Matrix $(d_{ij})_{m \times m}$ is irreducible. We have the following result.

Theorem 4.4. *Assume that there exists k such that $p_k > 0$. Then system (21) has no boundary equilibria. A unique positive equilibrium exists and is globally asymptotically stable in $\mathbb{R}_+^m$.*

Proof. Suppose that $p_k > 0$. It can be verified that system (21) has no boundary equilibria and the solutions are ultimately bounded. By Browder's Fixed Point Theorem [14], system (21) has a positive equilibrium $E^* = (x_1^*, x_2^*, \ldots, x_m^*)$. We will show E^* is globally asymptotically stable and thus unique.

Set $V_i(x_i) = x_i - x_i^* \ln x_i$. Then

$$\dot{V}_i = \frac{1}{x_i}(x_i - x_i^*)\Big(x_i f_i(x_i) + \sum_{j=1}^{m} d_{ij}x_j + p - qx_i\Big)$$

$$= (x_i - x_i^*)\Big(f_i(x_i) + \sum_{j=1}^{m} d_{ij}\frac{x_j}{x_i} + \frac{p}{x_i}$$

$$\quad - \frac{p}{x_i^*} - f_i(x_i^*) - \sum_{j=1}^{m} d_{ij}\frac{x_j^*}{x_i^*}\Big)$$

$$= (x_i - x_i^*)(f_i(x_i) - f_i(x_i^*)) - \frac{p}{x_i x_i^*}(x_i - x_i^*)^2$$

$$\quad + \sum_{j=1}^{m} d_{ij}x_j^*\Big(\frac{x_j}{x_j^*} - \frac{x_i}{x_i^*} + 1 - \frac{x_i^* x_j}{x_i x_j^*}\Big)$$

$$\leq \sum_{j=1}^{m} d_{ij}x_j^*\Big(\frac{x_j}{x_j^*} - \frac{x_i}{x_i^*} + 1 - \frac{x_i^* x_j}{x_i x_j^*}\Big).$$

Let $a_{ij} = d_{ij}x_j^*$, $F_{ij}(x_i, x_j) = \frac{x_j}{x_j^*} - \frac{x_i}{x_i^*} + 1 - \frac{x_i^* x_j}{x_i x_j^*}$, and $G_i(x_i) = -\frac{x_i}{x_i^*} + \ln \frac{x_i}{x_i^*}$. Then we have

$$\dot{V}_i \leq \sum_{j=1}^{m} a_{ij}F_{ij}(x_i, x_j)$$

$$= \sum_{j=1}^{m} a_{ij}\Big(G_i(x_i) - G_j(x_j) + 1 - \frac{x_i^* x_j}{x_i x_j^*} + \ln \frac{x_i^* x_j}{x_i x_j^*}\Big)$$

$$\leq \sum_{j=1}^{m} a_{ij}[G_i(x_i) - G_j(x_j)].$$

We have shown that V_i, F_{ij}, G_i, and a_{ij} satisfy the assumptions of Theorem 3.1 in [1]. Therefore, by Theorem 3.1 in [1]

$$V(x_1, \ldots, x_n) = \sum_{i=1}^{n} c_i V_i(x_i)$$

is a Lyapunov function for (16). It can be verified that $\dot{V} = 0 \Leftrightarrow x_i = x_i^*$, $i = 1, \ldots, m$, and thus E^* is globally asymptotically stable in $\mathbb{R}_+^m$. $\quad\square$

Let $p_i = \sum_{l \in V(\mathcal{G})\backslash H} d_{il}c_l$, and relabel entries in a strongly component H to be $1, 2, \ldots, m$. Then the H restricted system (20) is a special form of system (21). Applying Theorem 4.4, we have shown that assumption (A$_3$) is satisfied.

Let $\mathcal{P}$ be the set of equilibria of system (16), and $E : \mathcal{P} \to \mathbb{R}$ be the evaluation function defined as in Theorem 2.9. The following result follows from Theorem 2.9 and establishes the global convergence of all solutions of system (16).

Theorem 4.5. *All solutions of system (16) in the interior of region Δ converge to the unique maximizer of function E.*

We have the following results regarding the positivity of the globally attracting equilibrium E^* in Theorem 4.5.

Theorem 4.6. *Let E^* be the nonnegative globally asymptotically stable equilibrium of system (7). The following holds.*

(a) *If $s(A_f) \leq 0$, then $E^* = 0$ and the species goes to extinction in all patches.*

(b) *If $s(A_f) > 0$ and the dispersal matrix D is irreducible, then $E^* > 0$ and the species persists in all patches.*

(c) *If $s(A_f) > 0$ and the dispersal matrix D is reducible, then $E^* > 0$ if and only if $s(A_{f,H}) > 0$ for all minimal element H of $\mathcal{H}$.*

5. Numerical simulations

In this section we show several simulation results for the multi-group SEIR model in Section 2. We choose $n = 3$ and a bilinear incidence function $f_{ij}(S_i, I_j) = S_i I_j$. The transmission matrix $B = (\beta_{ij})_{3 \times 3}$ and its corresponding group-contact digraph are given in Fig. 2.

Here the transmission matrix (β_{ij}) is reducible. The set of strongly connected components $V(\mathcal{H}) = \{H_1, H_2\} = \{\{1, 2\}, 3\}$, and from the graph structure we know that $H_1 \prec H_2$, and H_1 is a minimal element. We can compute the basic reproduction number R_{0,H_i} for H_i reduced subsystem, $i = 1, 2$, using formula (10). Then, Theorem 3.3 implies that the basic reproduction number R_0 for the coupled system satisfies

$$R_0 = \max\{R_{0,H_1}, R_{0,H_2}\}.$$

With the bilinear incidence function $f_{ij}(S_i, I_j) = S_i I_j$, it can be verified that all assumptions (A$_1$)–(A$_5$) in Section 2 and (F$_1$)–(F$_6$) in Section 3 are satisfied. From Theorems 3.7 and 3.8 in Section 3, the global dynamics are determined by the two basic reproduction numbers, R_{0,H_1} and R_{0,H_2}, and the graph structure as summarized in the following three cases:

(1) When $R_{0,H_1} \leq 1$, $R_{0,H_2} \leq 1$, we have $R_0 \leq 1$, and $\pi(P^*)_{H_1} = \pi(P^*)_{H_2} = 0$. Accordingly, the disease-free equilibrium $P_0 = (S_1^*, 0, 0, S_2^*, 0, 0, S_3^*, 0, 0)$ is the only equilibrium and it is globally asymptotically stable.

(2) When $R_{0,H_1} \leq 1$, $R_{0,H_2} > 1$, we have $R_0 > 1$. There are two equilibria: the disease-free equilibrium P_0 with $\pi(P_0)_{H_1} = \pi(P_0)_{H_2} = 0$, and a mixed equilibrium $P^* = (S_1^*, 0, 0, S_2^*, 0, 0, S_3^*, E_3^*, I_3^*)$ with $\pi(P^*)_{H_1} = 0$ and $\pi(P^*)_{H_2} = 1$. Thus $E(P_0) = 0$ and $E(P^*) = 1$. The mixed equilibrium P^* is the maximizer of E, and all solutions in the interior of Δ converge to P^*.

(3) When $R_{0,H_1} > 1$, we have $R_0 > 1$. There are two possible equilibria: the disease-free equilibrium P_0 and a unique endemic equilibrium $P^* = (S_1^*, E_1^*, I_1^*, S_2^*, E_2^*, I_2^*, S_3^*, E_3^*, I_3^*)$ with $\pi(P^*)_{H_1} = \pi(P^*)_{H_2} = 1$. Thus $E(P_0) = 0$ and $E(P^*) = 2$. The endemic equilibrium P^* is the maximizer of E and attracts all solutions in the interior of Δ, irrespective of the value of R_{0,H_2}.
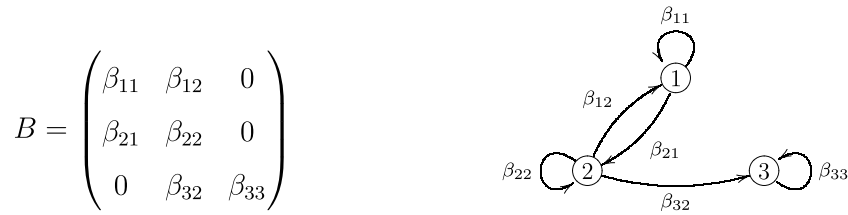
$$B = \begin{pmatrix} \beta_{11} & \beta_{12} & 0 \\ \beta_{21} & \beta_{22} & 0 \\ 0 & \beta_{32} & \beta_{33} \end{pmatrix}$$

Fig. 2. Transmission matrix B and the corresponding group-contact network $G(B)$.

(a) A positive solution converges to a mixed equilibrium in case (2).

(b) A positive solution converges to the endemic equilibrium in case (3).
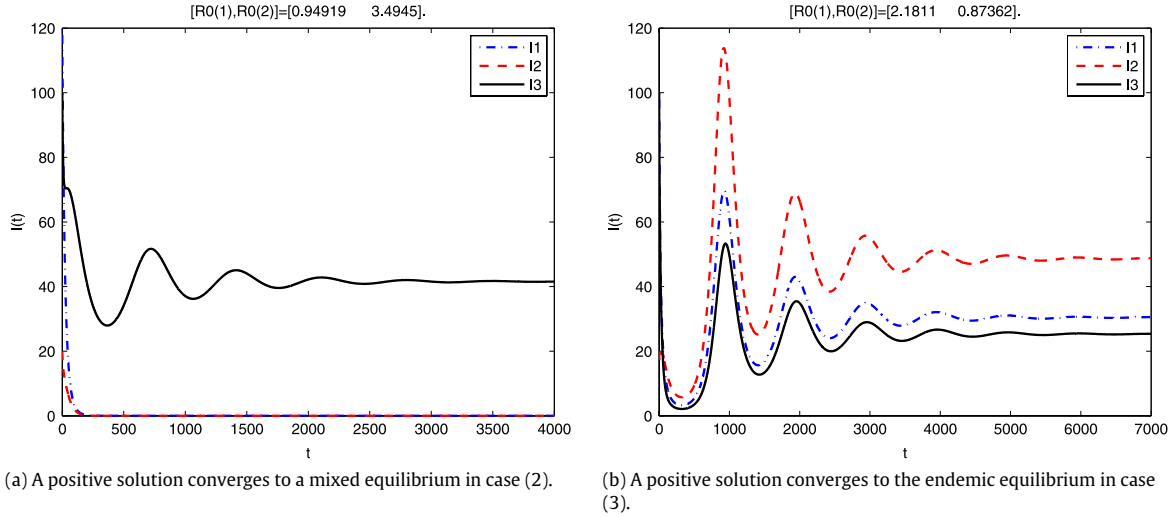
Fig. 3. Mixed equilibrium and positive equilibrium.

(a) A non-strongly connected network.

(b) A strongly connected network.
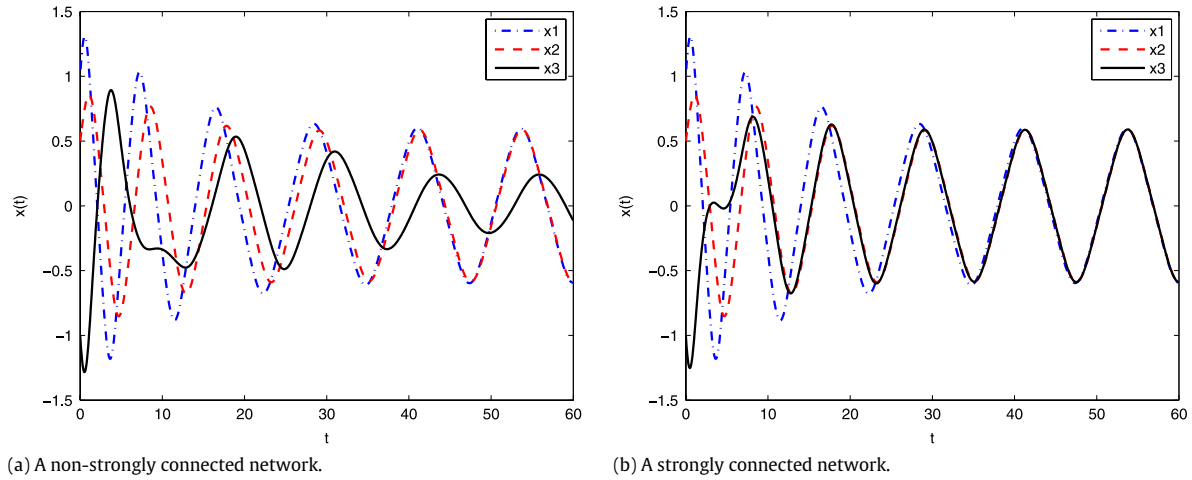
Fig. 4. Effect of network connectivity on synchronization of periodic solutions.

We have chosen parameter values to simulate the model and demonstrate the solutions for cases (2) and (3). Our simulation results are shown in Fig. 3, in which we have plotted $I_i(t)$ for $i = 1, 2, 3$. In Fig. 3(a), both $I_1(t)$ and $I_2(t)$ converge to zero, and $I_3(t)$ converges to a positive value, so that solutions with positive initial conditions converge to a mixed equilibrium. In Fig. 3(b), all $I_i(t)$ converge to a positive value and solutions with positive initial conditions converge to the endemic equilibrium. Note that in Fig. 3(b), the parameter values are chosen such that $R_{0,H_2} < 1$, however, $I_3(t)$ converge to positive values instead of 0.

We can see from the simulations that strongly connected components and the condensed graph play an important role to determine the global dynamics of coupled systems. Vertices in the same strongly connected component are synchronized. In the following

example, we demonstrate the impact of network connectivity on synchronization of oscillatory behaviours.

Consider a system of three coupled nonlinear oscillators:

$$\dot{x}_i = y_i,$$
$$\dot{y}_i = -x_i^3 - \sum_{j=1}^{n} a_{ij}(y_j - y_i). \quad i = 1, 2, 3. \tag{22}$$

If we choose a_{ij} the same form as in Fig. 2, then the connection graph is not strongly connected. The set of strongly connected components $V(\mathcal{H}) = \{H_1, H_2\} = \{\{1, 2\}, 3\}$. The simulation result in Fig. 4(a) shows x_1, x_2 are synchronized, and x_3 behaves differently. If we add an arc from vertex 3 to 2 ($\beta_{23} > 0$) in Fig. 2, then the connection graph becomes strongly connected, and the corresponding

simulation result is shown in Fig. 4(b). We can see that x_1, x_2, x_3 synchronize in this case. System (22) can also be regarded as a coupled cell network defined in [17]. When the nonzero weights a_{ij} are equal, synchronous oscillations observed in Fig. 4 can be explained by the symmetries in the network [18]. We refer the reader to the work of M. Golubitsky, I. Stewart and their collaborators [18,17] for the theory of coupled cell networks. Our simulations show that synchronous oscillations occur even when the weights a_{ij} are not equal and when symmetries are not present, suggesting that network connectivity may play a fundamental role in synchronous behaviours in complex networks.

Acknowledgements

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