Reaction-diffusion equations on graphs: stationary states and Lyapunov functions

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Abstract

Reaction-diffusion equations on graphs (networks) serve as mathematical models of various phenomena in physics and biology. We study the existence of spatially heterogeneous stationary states, provided that the diffusion coefficients are sufficiently small. We provide an easily applicable criterion for determining which of them are nonnegative. Next, we consider the problem of constructing Lyapunov functions for reaction-diffusion equations on graphs, provided that a Lyapunov function for the corresponding non-diffusive system is known. We provide an easy-to-use result applicable in situations where the non-diffusive Lyapunov function is a sum of univariate functions with nondecreasing derivatives. The results are illustrated by means of several examples from mathematical biology.

Keywords: reaction-diffusion equation, graph, network, spatially heterogeneous equilibrium, implicit function theorem, Lyapunov function, global stability, population dynamics, epidemic model

1 Introduction

Reaction-diffusion equations or systems are used to model a variety of phenomena in natural sciences; see [22] for a nice overview. In this paper, we focus on reaction-diffusion systems on discrete spatial domains represented by graphs (networks). In some situations, such systems are more natural than their continuous-space counterparts; for example, they are popular in mathematical biology, where the spatial domain consisting of discrete patches corresponds to fragmented habitats (such as islands, lakes connected by rivers, etc.). From the viewpoint of dynamical systems, it is interesting that the qualitative behavior of discrete-space systems is often strikingly different when compared to continuous-space systems. For example, the discrete-space Lotka-Volterra competition model has stable spatially heterogeneous stationary states [14, 19], unlike the continuous-space model, which has no stable nonconstant stationary states [9]. Another intriguing phenomenon is the existence of bichromatic and multichromatic traveling waves for lattice differential equations [7, 8], for which there is no counterpart on continuous-space domains.

We do not restrict ourselves to specific reaction functions (such as the frequently used logistic or Nagumo-type functions), but consider a general class of reaction-diffusion systems, which are obtained as follows. First, consider a dynamical system governed by a system of N scalar differential equations

$$(x_k)'(t) = h_k(x_1(t), \dots, x_N(t)), \quad k \in \{1, \dots, N\}. \tag{1.1}$$

Next, we take an arbitrary undirected graph (network) $G = (V(G), E(G))$, where $V(G) = \{1, \dots, n\}$ is a finite set of vertices, and $E(G)$ is a collection of undirected edges, i.e., unordered pairs of vertices from $V(G)$. The local dynamics inside each vertex will be driven by the above-mentioned N-dimensional dynamical system. Moreover, we suppose that these n systems are coupled via diffusion along the edges of G. In this way, we obtain the system of $n \cdot N$ reaction-diffusion equations

$$(x_k^i)'(t) = \sum_{j \in \mathcal{N}(i)} d_k^{ij}(x_k^j(t) - x_k^i(t)) + h_k(x_1^i(t), \dots, x_N^i(t)), \quad i \in V(G), \quad k \in \{1, \dots, N\}, \tag{1.2}$$

where $\mathcal{N}(i) = \{j \in V(G); \{i,j\} \in E(G)\}$ denotes the set of all neighbors of a vertex $i \in V(G)$, and $d_k^{ij} \geq 0$ is the intensity of diffusion for the k-th component of x from vertex j to vertex i (at this moment, we do not assume that the diffusion is symmetric, i.e., d_k^{ij} might differ from d_k^{ji}).

In the first part of the present paper (Section 2), we are concerned with the existence of spatially heterogeneous stationary states. Suppose that $\Sigma = \{S_1, \dots, S_s\} \subset \mathbb{R}^N$ is a finite set of stationary states of the original system 1.1. Then the diffusive system (1.2) has s stationary states in which no diffusion takes place, and $(x_1^i(t), \dots, x_N^i(t)) = S$ for a certain $S \in \Sigma$ and all $i \in V(G)$, $t \geq 0$; such stationary states are called spatially homogeneous. The system might also possess other stationary states, which are called spatially heterogeneous. (From now on, we omit the word "spatially", and simply refer to homogeneous and heterogeneous stationary states.) To see this, one can follow the idea from [17]: First, if $d_k^{ij} = 0$ for all i, j, k, we have n decoupled systems. For each $i \in V(G)$, we might choose an arbitrary $\sigma(i) \in \{1, \dots, s\}$, and let $(x_1^i(t), \dots, x_N^i(t)) = S_{\sigma(i)}$ for all $t \geq 0$. If $\sigma(1), \dots, \sigma(n)$ do not all coincide, we obtain a heterogeneous stationary state $S_\sigma = (S_{\sigma(1)}, \dots, S_{\sigma(n)})$ of (1.2). Now, if $h_1, \dots, h_N$ are smooth functions, and the Jacobian matrix J_h of $h = (h_1, \dots, h_N)$ is invertible at each of the points $S_{\sigma(1)}, \dots, S_{\sigma(n)}$, then the implicit function theorem guarantees that if d_k^{ij} are sufficiently small, then (1.2) still possesses a heterogeneous stationary state close to S_σ.

In some applications, we are interested only in stationary states with nonnegative components. For example, in the context of mathematical biology, we can consider a metapopulation consisting of N species living in n discrete patches – the vertices of G. The edges of G might correspond to the fact that the species can move between selected pairs of patches. Such a system can be modeled by equations of the form (1.2), where h_k describes the dynamics of the k-th species inside a single patch, and d_k^{ij} is the migration intensity for this species between vertices i and j. In this situation, it is clear that the only meaningful stationary states of (1.2) are those with nonnegative components.

Recall that the stationary states obtained using the implicit function theorem by continuation from S_σ depend continuously on the diffusion coefficients. Hence, if S_σ has strictly positive components, then the stationary state obtained by continuation from S_σ will be also positive, at least for sufficiently small d_k^{ij}. On the other hand, if at least one component of S_σ is strictly negative, it will remain negative for small d_k^{ij}. Hence, the only nontrivial case occurs if all components of S_σ are nonnegative, and at least one of them is zero. In such case, further analysis is needed to find out whether the corresponding stationary states obtained by continuation from S_σ have nonnegative components.

We focus on a certain class of right-hand sides $h_1, \dots, h_N$ and provide a simple criterion for checking whether the heterogeneous stationary states obtained by continuation from S_σ with at least one zero component remain nonnegative if the diffusion coefficients are small. The motivation comes from the paper [19] dealing with the Lotka-Volterra model of two competing species on graphs. The idea is as follows: To decide whether the continuation of S_σ has nonnegative components, we examine all vertices $i \in V(G)$. For each zero component of $S_{\sigma(i)}$, we determine the sign of the first nonvanishing derivative (with respect to the strength of the diffusion). The calculation in [19] (see Lemma 5.5 and Theorem 5.6 there) relies on implicit differentiation and the calculation of the inverse Jacobian matrix $J_h(S_{\sigma(i)})^{-1}$, which is easily accomplished in the two-dimensional case. Surprisingly, a similar calculation can be performed in a much more general setting, which is discussed in Section 2 of the present paper. Under suitable assumptions on the right-hand sides $h_1, \dots, h_N$, it turns out that it is possible to find the first nonvanishing derivative of the implicit function without having to calculate the inverse Jacobian matrix. Thus, the approach in the present paper is simpler and more general than in [19].

The landmark paper [14] by Levin also deals with stationary states of the Lotka-Volterra competition model on graphs. Levin focused on the case of two patches, and showed the existence of two stable nonnegative heterogeneous stationary states. He pointed out that his conclusions are valid also for more than two patches, and his Appendix 1 contains a "perturbation theorem" that provides sufficient conditions for the preservation of stable nonnegative equilibria under small changes of diffusion strength. Unfortunately, the paper contains no proof of the "perturbation theorem". Levin wrote it will appear in future, but it is unclear whether it was really published. In any case, Levin's theorem deals only with the situation when all $S_{\sigma(1)}, \dots, S_{\sigma(n)}$ are stable, while our present result applies to unstable equilibria as well.

Dynamical systems are often analyzed using Lyapunov functions, which are useful in the study of asymptotic behavior of solutions and global stability. Note also that the global stability of a homogeneous stationary state rules out the existence of heterogeneous stationary states. Recall that a Lyapunov function for the system (1.1) is a scalar function V, defined on a subset of $\mathbb{R}^N$, that has a unique global minimum and is nondecreasing along the trajectories of (1.1), i.e., its orbital derivative given by $\dot{V} = \nabla V \cdot h$ is nonnegative. In this situation, LaSalle's invariance principle provides sufficient conditions for the global asymptotic stability of the minimum of V.

Assuming that we have a Lyapunov function for the system (1.1), how to find a Lyapunov function for the diffusive system (1.2)? A fairly natural choice is to try the function

$$W(x^1, \dots, x^n) = \sum_{i \in V(G)} V(x_1^i, \dots, x_N^i). \tag{1.3}$$

In the second part of present paper (Section 3), we provide sufficient conditions guaranteeing that a function W constructed in this way is a Lyapunov function for (1.2).

Let us mention some related references. Lyapunov functions of the form (1.3) have appeared in several sources, e.g., in the context of Lotka-Volterra systems in [6], or in the analysis of the SIR epidemic model in [21]. A landmark paper dealing with Lyapunov functions for differential equations on graphs is [16], whose authors consider a much more general situation than we do here: Each vertex can have its own dynamics (i.e., the differential equations for the individual vertices are different), and also its own Lyapunov function. Moreover, the interaction between vertices is not limited to linear diffusion as in (1.2). Consequently, the main result of [16] has fairly complicated assumptions (involving the underlying graph G), which might be difficult to verify. Our goal here is to restrict the attention to systems of the form (1.2), and provide an easy-to-use result for the construction of Lyapunov functions of the form (1.3). In fact, although our main result can be derived as a consequence of the results in [16], it is easier to provide an independent proof. In our earlier paper [19] dealing with the Lotka-Volterra competition model, we have proved that for $N = 2$, the function W given by (1.3) is a Lyapunov function for the system (1.2) if V is a sum of constant terms, linear terms with nonnegative coefficients, and logarithmic terms with nonpositive coefficients. In Section 3, we generalize this result to the case when N is arbitrary and V is a sum of univariate functions with nondecreasing derivatives (such Lyapunov functions are common in mathematical biology).

The results of Sections 2 and 3 are illustrated on various examples from mathematical biology: several instances of the N-species Lotka-Volterra model, a model of two competing species with Allee effect, the Gause predator-prey model, SIR epidemic model, and SEIR epidemic model with nonlinear incidence rate.

2 Nonnegative stationary states

We begin with a few preliminaries. Throughout the rest of the paper, we always assume that G is a connected undirected graph (i.e., a graph where every two vertices are connected by a sequence of edges); otherwise, we can examine each connected component separately. We define the distance of arbitrary two vertices as the number of edges in a shortest path connecting these vertices. Also, for each $k \in \mathbb{N}_0$, we define the k-neighborhood of a vertex $i \in V(G)$ as the set $\mathcal{N}_k(i)$ consisting of all vertices whose distance from i does not exceed k. (In particular, $\mathcal{N}_0(i) = \{i\}$ and $\mathcal{N}_1(i) = \mathcal{N}(i) \cup \{i\}$ for all $i \in V(G)$.)

As in the introduction, we suppose that $h_1, \dots, h_N : \mathbb{R}^N \to \mathbb{R}^N$ are continuously differentiable functions, and $\Sigma = \{S_1, \dots, S_s\} \subset \mathbb{R}^N$ is a finite set of (not necessarily all) equilibrium points of the system (1.1) such that the Jacobian matrix J_h of $h = (h_1, \dots, h_N)$ is invertible at each $S \in \Sigma$.

To simplify the calculation, we will assume in this section that the diffusion coefficients in (1.2) have the form $d_k^{ij} = d\delta_k^{ij}$ for all i, j, k, where $\delta_k^{ij} > 0$ are fixed, and $d \geq 0$ is a variable. This means that the ratio of the diffusion coefficients is fixed, but their magnitudes are allowed to vary. Although this assumption might seem too restrictive, this setting suffices for determining the existence/nonexistence of heterogeneous stationary states with nonnegative components.

For each choice $S_\sigma = (S_{\sigma(1)}, \dots, S_{\sigma(n)}) \in \Sigma^n$, where $\sigma : \{1, \dots, n\} \to \{1, \dots, s\}$, the implicit function theorem guarantees the existence of an $\varepsilon > 0$ and continuously differentiable functions $u_k^i : [0, \varepsilon] \to \mathbb{R}$, $i \in V(G)$, $k \in \{1, \dots, N\}$, such that

$$\sum_{j \in \mathcal{N}(i)} d\delta_k^{ij}(u_k^i(d) - u_k^j(d)) = h_k(u_1^i(d), \dots, u_N^i(d)), \quad i \in V(G), \quad k \in \{1, \dots, N\}, \quad d \in [0, \varepsilon], \tag{2.1}$$

where $(u_1^i(0),\dots,u_N^i(0)) = S_{\sigma(i)}$ for all $i \in V(G)$. (Note that the Jacobian matrix of the system (1.2) with respect to $x_1^1,\dots,x_N^1,\dots,x_1^n,\dots,x_N^n$ evaluated at S_σ with $d_k^{ij}=0$ is the block diagonal matrix with the blocks $J_h(S_{\sigma(1)}),\dots,J_h(S_{\sigma(n)})$ on the diagonal, and this matrix is invertible because $J_h(S)$ is invertible for each $S \in \Sigma$. Hence, the assumptions of the implicit function theorem are satisfied.)

We keep in mind that the functions u_k^i depend on the choice of S_σ, although we do not write this dependence explicitly. Our goal is to determine whether all u_k^i are nonnegative on a right neighborhood of 0. Obviously, it suffices to focus on the case when S_σ is nonnegative and analyze only those u_k^i for which $u_k^i(0)=0$. The next lemma shows how to calculate the first nonvanishing derivative of such u_k^i at $d=0$.

Lemma 2.1. *Assume that $S_\sigma \in \Sigma^n$ is nonnegative, and $k \in \{1,\dots,N\}$, $i \in V(G)$, $\ell \in \mathbb{N}$ are such that the following conditions are satisfied:*

- $u_k^i(0) = 0$.
- *All vertices $j \in \mathcal{N}_{\ell-1}(i)$ have $u_k^j(0)=0$.*
- *Each of $h_1,\dots,h_N$ is ℓ times continuously differentiable at the points $S_{\sigma(1)},\dots,S_{\sigma(n)}$.*
- *If $q \in \{1,\dots,\ell\}$ and $m_1,\dots,m_q \in \{1,\dots,N\}\setminus\{k\}$, then $\frac{\partial^q h_k}{\partial x_{m_1}\cdots\partial x_{m_q}}(u_1^i(0),\dots,u_N^i(0)) = 0$.*

Then the following relations hold:

$$\begin{aligned}
(u_k^i)'(0) &= \dots = (u_k^i)^{(\ell-1)}(0) = 0,\\
(u_k^i)^{(\ell)}(0) &= \frac{-\ell}{\frac{\partial h_k}{\partial x_k}(u_1^i(0),\dots,u_N^i(0))}\sum_{j\in\mathcal{N}(i)} \delta_{ij}^k (u_k^j)^{(\ell-1)}(0)\\
&= \frac{(-1)^\ell \ell!}{\left(\frac{\partial h_k}{\partial x_k}(u_1^i(0),\dots,u_N^i(0))\right)^\ell}\sum_{i_1\in\mathcal{N}(i)}\sum_{i_2\in\mathcal{N}(i_1)}\cdots\sum_{i_\ell\in\mathcal{N}(i_{\ell-1})} \delta_{ii_1}^k\cdots\delta_{i_{\ell-1}i_\ell}^k u_k^{i_\ell}(0).
\end{aligned}\tag{2.2}$$

Consequently, if $\mathcal{N}_\ell(i)$ contains a vertex j with $u_k^j(0)>0$, then the sign of $(u_k^i)^{(\ell)}(0)$ coincides with the sign of

$$\left(-\frac{\partial h_k}{\partial x_k}(u_1^i(0),\dots,u_N^i(0))\right)^\ell.$$

Proof. First, we show that the statement holds for $\ell=1$. Hence, we assume that $i\in V(G)$, $k\in\{1,\dots,N\}$ are such that $u_k^i(0)=0$, and our goal is to calculate $(u_k^i)'(0)$.

Differentiation of (2.1) with respect to d gives

$$\sum_{j\in\mathcal{N}(i)} \delta_k^{ij}(u_k^i(d)-u_k^j(d)) + \sum_{j\in\mathcal{N}(i)} d\delta_k^{ij}((u_k^i)'(d)-(u_k^j)'(d)) = \sum_{m=1}^N \frac{\partial h_k}{\partial x_m}(u_1^i(d),\dots,u_N^i(d))(u_m^i)'(d). \tag{2.3}$$

By the assumptions, we have

$$\frac{\partial h_k}{\partial x_m}(u_1^i(0),\dots,u_N^i(0)) = 0 \quad \text{for all } m\in\{1,\dots,N\}\setminus\{k\}.$$

Thus, substituting $d=0$ into (2.3), we obtain

$$-\sum_{j\in\mathcal{N}(i)} \delta_k^{ij} u_k^j(0) = \frac{\partial h_k}{\partial x_k}(u_1^i(0),\dots,u_N^i(0))(u_k^i)'(0),$$

or equivalently

$$(u_k^i)'(0) = \frac{-1}{\frac{\partial h_k}{\partial x_k}(u_1^i(0),\dots,u_N^i(0))}\sum_{j\in\mathcal{N}(i)} \delta_k^{ij} u_k^j(0).$$

Note that $\frac{\partial h_k}{\partial x_k}(u_1^i(0),\dots,u_N^i(0)) \neq 0$, for otherwise the k-th row of $J_h(u_1^i(0),\dots,u_N^i(0))$ would be zero, and the matrix would not be invertible. This completes the proof for $\ell = 1$.

Next, suppose that the statement of the lemma is valid for $\ell - 1$, and let us prove it for $\ell \geq 2$. Hence, we now assume that all vertices $j \in \mathcal{N}_{\ell-1}(i)$ have $u_k^j(0) = u_k^i(0) = 0$. By the induction hypothesis, we know that

$$(u_k^i)'(0) = \cdots = (u_k^i)^{(\ell-2)}(0) = 0, \qquad (u_k^i)^{(\ell-1)}(0) = \frac{-(\ell-1)}{\frac{\partial h_k}{\partial x_k}(u_1^i(0),\dots,u_N^i(0))} \sum_{j\in\mathcal{N}(i)} \delta_k^{ij} (u_k^j)^{(\ell-2)}(0).$$

If $j \in \mathcal{N}(i)$, then $\mathcal{N}_{\ell-2}(j)$ is a subset of $\mathcal{N}_{\ell-1}(i)$, which contains only vertices m with $u_k^m(0) = 0$. Hence, by induction hypothesis, $(u_k^j)^{(\ell-2)}(0) = 0$ for each $j \in \mathcal{N}(i)$. Consequently,

$$(u_k^i)^{(\ell-1)}(0) = 0.$$

To calculate $(u_k^i)^{(\ell)}(0)$, we consider the ℓ-th derivative of (2.1) with respect to d. When differentiating the left-hand side of (2.1), the Leibniz rule for the ℓ-th derivative yields the expression

$$\sum_{j\in\mathcal{N}(i)} d\delta_k^{ij} \left((u_k^i)^{(\ell)}(d) - (u_k^j)^{(\ell)}(d)\right) + \ell \sum_{j\in\mathcal{N}(i)} \delta_k^{ij} \left((u_k^i)^{(\ell-1)}(d) - (u_k^j)^{(\ell-1)}(d)\right).$$

Letting $d = 0$ and recalling that $(u_k^i)^{(\ell-1)}(0) = 0$, we get

$$-\ell \sum_{j\in\mathcal{N}(i)} \delta_k^{ij} (u_k^j)^{(\ell-1)}(0). \tag{2.4}$$

The ℓ-th derivative of the right-hand side of (2.1) is a sum of terms having the form

$$\frac{\partial^q h_k}{\partial x_{m_1}\cdots\partial x_{m_q}}(u_1^i(d),\dots,u_N^i(d))(u_{m_1}^i)^{(\ell_1)}(d)\cdots(u_{m_q}^i)^{(\ell_q)}(d), \tag{2.5}$$

where $q \in \{1,\dots,\ell\}$, $m_1,\dots,m_q \in \{1,\dots,N\}$, and $\ell_1,\dots,\ell_n \in \mathbb{N}$ satisfy $\ell_1 + \cdots + \ell_q = \ell$. In particular, terms corresponding to $q = 1$ are $\sum_{m=1}^N \frac{\partial h_k}{\partial x_m}(u_1^i(d),\dots,u_N^i(d))(u_m^i)^{(\ell)}(d)$; if $d = 0$, this sum reduces to

$$\frac{\partial h_k}{\partial x_k}(u_1^i(0),\dots,u_N^i(0))(u_k^i)^{(\ell)}(0). \tag{2.6}$$

All remaining terms of the form (2.5) have $q \geq 2$ and $\ell_1,\dots,\ell_q \leq \ell-1$; hence, if k is among $m_1,\dots,m_q$, then the value of (2.5) at $d = 0$ is zero because $(u_k^i)'(0) = \cdots = (u_k^i)^{(\ell-1)}(0) = 0$. On the other hand, if k is not among $m_1,\dots,m_q$, then the value of (2.5) at $d = 0$ is also zero because $\frac{\partial^q h_k}{\partial x_{m_1}\cdots\partial x_{m_q}}(u_1^i(0),\dots,u_N^i(0)) = 0$ by the assumption of the lemma. Thus, we see that the ℓ-th derivative of the right-hand side of (2.1) at $d = 0$ is simply (2.6). Equating (2.4) and (2.6), we obtain the desired relation

$$(u_k^i)^{(\ell)}(0) = \frac{-\ell}{\frac{\partial h_k}{\partial x_k}(u_1^i(0),\dots,u_N^i(0))} \sum_{j\in\mathcal{N}(i)} \delta_k^{ij} (u_k^j)^{(\ell-1)}(0).$$

To obtain the alternative formula (2.2) for $(u_k^i)^{(\ell)}(0)$, observe that for each $j \in \mathcal{N}(i)$, $\mathcal{N}_{\ell-2}(j)$ is a subset of $\mathcal{N}_{\ell-1}(i)$, and therefore contains only vertices m with $u_k^m(0) = 0$. Hence, we have

$$(u_k^j)^{(\ell-1)}(0) = \frac{-(\ell-1)}{\frac{\partial h_k}{\partial x_k}(u_1^i(0),\dots,u_N^i(0))} \sum_{m\in\mathcal{N}(j)} \delta_k^{jm} (u_k^m)^{(\ell-2)}(0),$$

and consequently

$$(u_k^i)^{(\ell)}(0) = \frac{\ell(\ell-1)}{\left(\frac{\partial h_k}{\partial x_k}(u_1^i(0),\dots,u_N^i(0))\right)^2} \sum_{j\in\mathcal{N}(i)} \sum_{m\in\mathcal{N}(j)} (-\delta_k^{ij})(-\delta_k^{jm})(u_k^m)^{(\ell-2)}(0).$$

Continuing in a similar way, we can rewrite the inner sum as a double sum of derivatives of order $\ell-3$, etc. Finally, we arrive at the formula

$$(u_k^i)^{(\ell)}(0) = \frac{(-1)^\ell \ell!}{\left(\frac{\partial h_k}{\partial x_k}(u_1^i(0),\dots,u_N^i(0))\right)^\ell} \sum_{i_1\in\mathcal{N}(i)} \sum_{i_2\in\mathcal{N}(i_1)} \cdots \sum_{i_\ell\in\mathcal{N}(i_{\ell-1})} \delta_k^{ii_1}\cdots\delta_k^{i_{\ell-1}i_\ell} u_k^{i_\ell}(0).$$

If $\mathcal{N}_\ell(i)$ contains a vertex j with $u_k^j(0)>0$, then the ℓ-fold sum on the right-hand side is positive, and the sign of $(u_k^i)^{(\ell)}(0)$ coincides with the sign of the fraction before the sum, which is the same as the sign of

$$\left(-\frac{\partial h_k}{\partial x_k}(u_1^i(0),\dots,u_N^i(0))\right)^\ell. \qquad \square$$

The next theorem provides a criterion for determining whether the continuation of S_σ has nonnegative components. We keep the same notation as in the beginning of this section, i.e., the functions u_k^i, $i\in V(G)$, $k\in\{1,\dots,N\}$, which are defined for all sufficiently small $d\ge 0$, are the components of the continuation of S_σ obtained from the implicit function theorem. The symbol diam G denotes the diameter of a graph G, i.e., the maximum distance between two vertices in G. Let us also recall the concept of a real analytic function: We say that $h:\mathbb{R}^n\to\mathbb{R}$ is real analytic at a point $x_0\in\mathbb{R}^n$ if it can be expressed as a convergent power series in n variables in a certain neighborhood of x_0.

Theorem 2.2. *Suppose that $S_\sigma\in\Sigma^n$ has nonnegative components, each of $h_1,\dots,h_N$ is real analytic at the points $S_{\sigma(1)},\dots,S_{\sigma(n)}$, and if $k\in\{1,\dots,N\}$ and $i\in V(G)$ are such that $u_k^i(0)=0$, then $\frac{\partial^q h_k}{\partial x_{m_1}\cdots\partial x_{m_q}}(u_1^i(0),\dots,u_N^i(0))=0$ for all $q\in\{1,\dots,\operatorname{diam} G\}$ and $m_1,\dots,m_q\in\{1,\dots,N\}\setminus\{k\}$.*

Then the continuation of S_σ is nonnegative for all sufficiently small $d>0$ if and only if for each $k\in\{1,\dots,N\}$ and $i\in V(G)$ for which $u_k^i(0)=0$, we have either $u_k^j(0)=0$ for all $j\in V(G)$, or $\frac{\partial h_k}{\partial x_k}(u_1^i(0),\dots,u_N^i(0))<0$.

Proof. The assumption that $h_1,\dots,h_N$ are real analytic at $S_{\sigma(1)},\dots,S_{\sigma(n)}$ guarantees that all functions u_k^i, $k\in\{1,\dots,N\}$, $i\in V(G)$, are real analytic at 0 (see the real analytic implicit function theorem in [13, Theorem 1.8.3]).

Let us begin by proving that the above-mentioned condition is sufficient for the nonnegativity of $(u_1^1(d),\dots,u_N^1(d),\dots,u_1^n(d),\dots,u_N^n(d))$ for d in a right neighborhood of 0. It suffices to show the nonnegativity of those components u_k^i for which $u_k^i(0)=0$. If $u_k^j(0)=0$ for all $j\in V(G)$, then Lemma 2.1 implies that all derivatives of u_k^i at 0 vanish, and therefore u_k^i must be identically zero since it is real analytic. On the other hand, if it is not true that $u_k^j(0)=0$ for all $j\in V(G)$, but we have $\frac{\partial h_k}{\partial x_k}(u_1^i(0),\dots,u_N^i(0))<0$, then Lemma 2.1 implies that the first nonzero derivative of u_k^i at 0 is positive, and therefore u_k^i is nonnegative in a right neighborhood of 0.

To prove the necessity of the above-mentioned condition, assume that there exist $k\in\{1,\dots,N\}$ and $i\in V(G)$ such that $u_k^i(0)=0$, but $\frac{\partial h_k}{\partial x_k}(u_1^i(0),\dots,u_N^i(0))\ge 0$ and not all $j\in V(G)$ have $u_k^j(0)=0$. In fact, we know from the proof of Lemma 2.1 that $\frac{\partial h_k}{\partial x_k}(u_1^i(0),\dots,u_N^i(0))$ cannot be zero (otherwise $J_h(u_1^i(0),\dots,u_N^i(0))$ would not be invertible), and therefore must be strictly positive. We choose a $j\in V(G)$ such that $u_k^j(0)>0$, and the distance ℓ between i and j is as small as possible. If ℓ is odd, then Lemma 2.1 implies $u_k^i(0)=(u_k^i)'(0)=\cdots=(u_k^i)^{(\ell-1)}(0)=0$ and $(u_k^i)^{(\ell)}(0)<0$, which means that u_k^i is negative on a right neighborhood of 0. If ℓ is even, then $\ell\ge 2$, and i has a neighbor $m\in\mathcal{N}(i)$ whose distance from j is $\ell-1$. Since $\mathcal{N}_{\ell-2}(j)\subset\mathcal{N}_{\ell-1}(i)$, Lemma 2.1 implies that $u_k^m(0)=(u_k^m)'(0)=\cdots=(u_k^m)^{(\ell-2)}(0)=0$ and $(u_k^m)^{(\ell-1)}(0)<0$. Thus, u_k^m is negative on a right neighborhood of 0. $\square$

If the assumptions of Theorem 2.2 are satisfied, we see that the fact whether the continuation of S_σ is nonnegative depends only on the set $\{\sigma(i): i=1,\dots,n\}$, i.e., on the range of σ, and not on the distribution of the values $\sigma(1),\dots,\sigma(n)$ among the vertices, i.e., on the mapping σ itself. This leads us to the following concept of an admissible set – a set of equilibria of (1.1) that can be combined together in an arbitrary way in order to get a nonnegative stationary state of the spatial system (1.2) for small $d\ge 0$. Note that the definition makes sense because we are considering reaction-diffusion systems with the same reaction function (and therefore the same equilibrium points) at each vertex.

Definition 2.3. If $\Sigma = \{S_1, \dots, S_s\} \subset \mathbb{R}^N$ is a finite set of stationary states of the system (1.1), we say that $\mathcal{A} \subset \Sigma$ is an *admissible set* for (1.2) if it has the following property: If $S_{\sigma(1)}, \dots, S_{\sigma(n)} \in \mathcal{A}$, then the continuation of $S_\sigma = (S_{\sigma(1)}, \dots, S_{\sigma(n)})$ is nonnegative for small $d \geq 0$.

We say that an admissible set $\mathcal{A}$ is *maximal* if it is not contained in any larger admissible set.

Note that each admissible set contains only nonnegative states S_i, and each nonnegative state S_i gives rise to the singleton admissible set $\mathcal{A} = \{S_i\}$, but it need not be maximal.

It follows from Theorem 2.2 that the problem of determining all choices $\sigma(1), \dots, \sigma(n) \in \{1, \dots, s\}$ such that the continuation of $S_\sigma = (S_{\sigma(1)}, \dots, S_{\sigma(n)})$ is nonnegative can be solved by finding all maximal admissible sets for (1.2). In particular, all $S_{\sigma(1)}, \dots, S_{\sigma(n)}$ have to be elements of a certain maximal admissible set.

The next result provides a formula for the number of nonnegative heterogeneous stationary states; the symbol $|X|$ stands for the number of elements of a set X.

Theorem 2.4. *Suppose that $\mathcal{A}_1$, ..., $\mathcal{A}_r$ is the collection of all distinct maximal admissible sets for the system* (1.2)*. Assume that $|\mathcal{A}_i \cap \mathcal{A}_j| \leq 1$ whenever $i \neq j$.*

Then, if $d_k^{ij} = d\delta_k^{ij}$ for all i, j, k, the system (1.2) *has at least*

$$\sum_{i=1}^{r} (|\mathcal{A}_i|^n - |\mathcal{A}_i|) \tag{2.7}$$

nonnegative heterogeneous stationary states for all sufficiently small $d \geq 0$.

Proof. Note that each $\mathcal{A}_i$ gives rise to $|\mathcal{A}_i|^n$ nonnegative stationary states, with $|\mathcal{A}_i|^n - |\mathcal{A}_i|$ of them being heterogeneous. Therefore, if $\mathcal{A}_1$, ..., $\mathcal{A}_r$ are pairwise disjoint, then the system (1.2) with $d_k^{ij} = d\delta_k^{ij}$ for all i, j, k has at least

$$\sum_{i=1}^{r} (|\mathcal{A}_i|^n - |\mathcal{A}_i|)$$

nonnegative heterogeneous states for all sufficiently small $d \geq 0$. The formula is still correct in the more general case when the intersection of any two sets $\mathcal{A}_i$ and $\mathcal{A}_j$ contains at most one element. Indeed, if $S_{\sigma(1)}, \dots, S_{\sigma(n)} \in \mathcal{A}_i \cap \mathcal{A}_j$ with $i \neq j$, it follows that $S_{\sigma(1)} = \dots = S_{\sigma(n)}$, and therefore each heterogeneous state is counted only once in (2.7). $\square$

In general, the number (2.7) is only a lower bound, since (1.2) might possess other heterogeneous stationary states besides those obtained from the implicit function theorem by continuation from S_σ with $\sigma(1), \dots, \sigma(n) \in \{1, \dots, s\}$.

Let us emphasize that throughout this paper, we always assume that the vertices of G are labeled by natural numbers $1, \dots, n$, i.e., they are distinguishable. In the unlabeled case, the formula (2.7) is no longer valid for graphs possessing symmetries (i.e., nontrivial automorphisms).

Remark 2.5. Apart from determining whether a heterogeneous stationary state obtained by continuation from S_σ has nonnegative components, we might be also interested in the stability of such state. Assume that $S_{\sigma(1)}, \dots, S_{\sigma(n)}$ are hyperbolic equilibria of (1.1), i.e., $J_h(S_\sigma(1))$, ..., $J_h(S_\sigma(n))$ have only eigenvalues with nonzero real parts. The Jacobian matrix of the system (1.2) with $d_k^{ij} = 0$ is a block diagonal matrix with the blocks $J_h(S_{\sigma(1)}), \dots, J_h(S_{\sigma(n)})$ on the diagonal. Hence, it is clear that the equilibrium S_σ of (1.2) is stable if and only if $S_{\sigma(1)}, \dots, S_{\sigma(n)}$ are stable equilibria of (1.1).

For small diffusion coefficients, the Jacobian matrix of (1.2) at the state obtained by continuation from S_σ will be a small perturbation of the previously mentioned Jacobian matrix at S_σ, and will have the same number of eigenvalues with positive/negative real parts (because the eigenvalues depend continuously on the matrix entries). Hence, this perturbed stationary state is stable if and only if $S_{\sigma(1)}, \dots, S_{\sigma(n)}$ are stable equilibria of (1.1).

Similarly to Theorem 2.4, an admissible set $\mathcal{A}$ (not necessarily maximal) containing only stable states of the non-spatial system (1.1) gives rise to $|\mathcal{A}|^n$ nonnegative stable stationary states of the spatial system (1.2), with $|\mathcal{A}|^n - |\mathcal{A}|$ of them being heterogeneous.

Remark 2.6. Since we are interested only in the stationary states, the results presented in this section apply not only to differential equations, but also to difference equations of the form

$$(x_k^i)(t+1) - (x_k^i)(t) = \sum_{j \in \mathcal{N}(i)} d_k^{ij}(x_k^j(t) - x_k^i(t)) + h_k(x_1^i(t), \dots, x_N^i(t)), \quad i \in V(G), \quad k \in \{1, \dots, N\}$$

(or, more generally, to dynamic equations on time scales).

Let us illustrate the theoretical results on several examples. We begin with the scalar reaction-diffusion equation.

Example 2.7. In the simplest situation when $N = 1$, the system (1.1) reduces to the single equation $x'(t) = h(x(t))$, and (1.2) becomes the scalar reaction-diffusion equation

$$(x^i)'(t) = \sum_{j \in \mathcal{N}(i)} d^{ij}(x^j(t) - x^i(t)) + h(x^i(t)), \quad i \in V(G). \tag{2.8}$$

We suppose that $h : \mathbb{R} \to \mathbb{R}$ has the zero equilibrium and several positive equilibria, i.e., $\Sigma = \{S_1, S_2, \dots, S_s\}$ with $0 = S_1 < S_2 < \dots < S_s$. To be able to apply Theorem 2.2, we assume that $d^{ij} = d\delta^{ij}$ and that for each $x \in \Sigma$, h is real analytic at x and $h'(x) \neq 0$.

An arbitrary $S_\sigma = (S_{\sigma(1)}, \dots, S_{\sigma(n)}) \in \Sigma^n$ is a stationary state for (2.8) with $d^{ij} = 0$. If $S_{\sigma(i)} \neq 0$ for all $i \in V(G)$, then it is clear that the continuation of S_σ is nonnegative for small $d > 0$. If $S_{\sigma(i)} = 0$ for some $i \in V(G)$, Theorem 2.2 implies that the continuation of S_σ is nonnegative for small $d > 0$ if and only if either $S_{\sigma(j)} = 0$ for all $j \in V(G)$, or $h'(0) < 0$. In other words, if $h'(0) < 0$, then the unique maximal admissible set for (2.8) is Σ and we get $s^n - s$ nonnegative heterogeneous stationary states, while if $h'(0) > 0$, then the maximal admissible sets are $\mathcal{A}_1 = \{0\}$ and $\mathcal{A}_2 = \{S_2, \dots, S_s\}$, and we get $(s-1)^n - (s-1)$ nonnegative heterogeneous stationary states.

For example, if $h(x) = \rho x(x-a)(b-x)$, where $0 < a < b$, then (2.8) is the Nagumo equation considered in [20]. We have $\Sigma = \{0, a, b\}$, $h'(a) = \rho a(b-a) \neq 0$, $h'(b) = \rho b(a-b) \neq 0$ and $h'(0) = -\rho ab < 0$. Hence, the unique maximal admissible set is Σ, and we get $3^n - 3$ nonnegative heterogeneous stationary states for $d^{ij} = d\delta^{ij}$ and small $d > 0$, as proved in [20].

On the other hand, consider the logistic nonlinearity $h(x) = \rho x(a-x)$, where $a > 0$. Then $\Sigma = \{0, a\}$, $h'(a) = -\rho a \neq 0$, and $h'(0) = \rho a > 0$. Hence, the maximal admissible sets are $\mathcal{A}_1 = \{0\}$, $\mathcal{A}_2 = \{a\}$, which lead only to homogeneous stationary states.

The next two examples are related to the N-species Lotka-Volterra model

$$x_k'(t) = \rho_k x_k(t) \left(1 - \sum_{j=1}^{N} b_{kj} x_j(t)\right), \quad k \in \{1, \dots, N\}, \tag{2.9}$$

where b_{kj} are real parameters (depending on their signs, we get a predator-prey/competition/cooperative model). We focus on the corresponding reaction-diffusion equations

$$(x_k^i)'(t) = \sum_{j \in \mathcal{N}(i)} d_k^{ij}(x_k^j(t) - x_k^i(t)) + \rho_k x_k^i(t) \left(1 - \sum_{j=1}^{N} b_{kj} x_j^i(t)\right), \quad i \in V(G), \quad k \in \{1, \dots, N\}. \tag{2.10}$$

The reaction functions are

$$h_k(x_1, \dots, x_N) = \rho_k x_k \left(1 - \sum_{j=1}^{N} b_{kj} x_j\right),$$

and it is common to assume that $b_{kk} = 1$ for all $k \in \{1, \dots, N\}$. Then we have

$$\frac{\partial h_k}{\partial x_j}(x_1, \dots, x_N) = \begin{cases} -b_{kj}\rho_k x_k & \text{for } j \in \{1, \dots, N\} \setminus \{k\}, \\ \rho_k \left(1 - \sum_{j=1}^{N} b_{kj} x_j - x_k\right) & \text{for } j = k. \end{cases}$$

Hence, if $x_k = 0$, then $\frac{\partial^q h_k}{\partial x_{m_1} \cdots \partial x_{m_q}}(x_1, \dots, x_N) = 0$ for all $q \in \mathbb{N}$ and $m_1, \dots, m_q \in \{1, \dots, N\} \setminus \{k\}$, i.e., the condition from Theorem 2.2 is satisfied. Note also that $h_1, \dots, h_N$ are real analytic in $\mathbb{R}^N$.

We begin with an observation concerning the zero (extinction) equilibrium.

Remark 2.8. The origin $S_0 = (0, \dots, 0) \in \mathbb{R}^N$ is always an equilibrium point of (2.9). Suppose that there are other equilibria $S_1, \dots, S_s \in \mathbb{R}^N$ with nonnegative components such that the Jacobian matrix J_h of $h = (h_1, \dots, h_N)$ is invertible at each S_i. In this situation, we have $\Sigma = \{S_0, \dots, S_s\}$.

Then $S_\sigma = (S_{\sigma(1)}, \dots, S_{\sigma(n)}) \in \Sigma^n$ is a stationary state of (2.10) with $d_k^{ij} = 0$, and we want to know whether the continuation of S_σ is nonnegative for $d_k^{ij} = d\delta_k^{ij}$ and small $d > 0$. Let us focus on the case when $S_{\sigma(i)} = S_0$ for some $i \in V(G)$. Choose an arbitrary $k \in \{1, \dots, N\}$. Since $u_k^i(0) = 0$ and $\frac{\partial h_k}{\partial x_k}(S_0) = \rho_k > 0$, Theorem 2.2 implies that a necessary condition for the continuation of S_σ to be nonnegative is that $u_k^j(0) = 0$ for all $j \in V(G)$. This proves that if $S_{\sigma(i)} = S_0$ for some $i \in V(G)$, the continuation of S_σ is nonnegative if and only if $\sigma(1) = \cdots = \sigma(n)$, i.e., S_σ is the extinction equilibrium.

We now consider the Lotka-Volterra model of two competing species. Although it is quite simple and not too realistic, we will see that its diffusive version already possesses heterogeneous stationary states.

Example 2.9. The classical Lotka-Volterra model of two competing species is a special case of (2.9) with $N = 2$. It has the form

$$\begin{aligned} x'(t) &= \rho_1 x(t)(1 - x(t) - \alpha y(t)), \\ y'(t) &= \rho_2 y(t)(1 - \beta x(t) - y(t)). \end{aligned} \tag{2.11}$$

where α, β are positive parameters, which we assume to be distinct from 1. The corresponding reaction-diffusion equations are

$$\begin{aligned} (x^i)'(t) &= \sum_{j \in \mathcal{N}(i)} d_1^{ij}(x^j(t) - x^i(t)) + \rho_1 x^i(t)(1 - x^i(t) - \alpha y^i(t)), \qquad i \in V(G), \\ (y^i)'(t) &= \sum_{j \in \mathcal{N}(i)} d_2^{ij}(y^j(t) - y^i(t)) + \rho_2 y^i(t)(1 - \beta x^i(t) - y^i(t)), \qquad i \in V(G). \end{aligned} \tag{2.12}$$

The equilibria of (2.11) are

$$S_0 = (0,0), \quad S_1 = (1,0), \quad S_2 = (0,1), \quad S_3 = \left(\frac{1-\alpha}{1-\alpha\beta}, \frac{1-\beta}{1-\alpha\beta} \right),$$

where S_3 is relevant if and only if $\alpha > 1$ and $\beta > 1$, or $\alpha < 1$ and $\beta < 1$ (otherwise it has negative components). Using the reaction functions $h_1(x,y) = \rho_1 x(1 - x - \alpha y)$ and $h_2(x,y) = \rho_2 y(1 - \beta x - y)$, we can calculate the Jacobian determinants

$$\begin{aligned} \det J_h(S_0) &= \rho_1\rho_2, \\ \det J_h(S_1) &= \rho_1\rho_2(\beta - 1), \\ \det J_h(S_2) &= \rho_1\rho_2(\alpha - 1), \\ \det J_h(S_3) &= \rho_1\rho_2 \frac{(\alpha-1)(\beta-1)}{1-\alpha\beta} \end{aligned}$$

to see that the Jacobian matrices $J_h(S_0)$, $J_h(S_1)$, $J_h(S_2)$, $J_h(S_3)$ are invertible.

Let us find all maximal admissible sets for (2.12). By Remark 2.8, one maximal admissible set is $\{S_0\}$, and it remains to consider subsets of $\{S_1, S_2, S_3\}$. For this reason, we consider $S_\sigma = (S_{\sigma(1)}, \dots, S_{\sigma(n)})$ with $\sigma(1), \dots, \sigma(n) \in \{1, 2, 3\}$, and choose an arbitrary $i \in V(G)$. We need to check the cases when $S_{\sigma(i)}$ has a zero component, i.e., $\sigma(i) \in \{1, 2\}$.

If $\sigma(i) = 1$, then $u_2^i(0) = 0$. We have $\frac{\partial h_2}{\partial y}(S_1) = \rho_2(1 - \beta)$, which is negative if and only if $\beta > 1$. For $\beta < 1$, Theorem 2.2 requires $u_2^j(0) = 0$ for all $j \in V(G)$, which happens only if $\sigma(j) = 1$ for all $j \in V(G)$.

Similarly, if $\sigma(i) = 2$, then $u_1^i(0) = 0$. Since $\frac{\partial h_1}{\partial x}(S_2) = \rho_1(1 - \alpha)$, Theorem 2.2 requires either $\alpha > 1$, or $\sigma(j) = 2$ for all $j \in V(G)$.

To sum up, Theorem 2.2 implies that the continuation of S_σ is nonnegative if and only if S_σ is a homogeneous stationary state, or if $\alpha > 1$, $\beta > 1$ and $\sigma(i) \in \{1, 2, 3\}$ for all $i \in V(G)$. This confirms the results obtained in [19, Theorem 5.6], where it was shown that (2.12) has no heterogeneous stationary states except when $\alpha > 1$ and $\beta > 1$. We are now able to determine the maximal admissible sets for (2.12): If $\alpha, \beta < 1$, we have the admissible sets

$$\mathcal{A}_1 = \{S_0\}, \quad \mathcal{A}_2 = \{S_1\}, \quad \mathcal{A}_3 = \{S_2\}, \quad \mathcal{A}_4 = \{S_3\},$$

leading only to 4 homogeneous stationary states.

If exactly one of α, β is greater than 1, then the maximal admissible sets are

$$\mathcal{A}_1 = \{S_0\}, \quad \mathcal{A}_2 = \{S_1\}, \quad \mathcal{A}_3 = \{S_2\},$$

leading only to 3 homogeneous stationary states.

Finally, if $\alpha > 1$ and $\beta > 1$, then the maximal admissible sets are

$$\mathcal{A}_1 = \{S_0\}, \quad \mathcal{A}_2 = \{S_1, S_2, S_3\}.$$

In the last case, we conclude (cf. the formula (2.7)) that the system (2.12) with $d_k^{ij} = d\delta_k^{ij}$ has $3^n - 3$ nonnegative heterogeneous stationary states for all sufficiently small $d > 0$.

For example, the two-patch model ($n = 2$) has 6 heterogeneous nonnegative equilibria (as well as 4 homogeneous equilibria) for small diffusion. Note that page 217 of Levin's paper [14] cited in the introduction incorrectly says there are only 2 heterogeneous equilibria corresponding to $\sigma(1) = 1$ and $\sigma(2) = 2$, or vice versa. The existence of 6 heterogeneous nonnegative equilibria is easily confirmed by numerical calculation.

Biological interpretation. The biological meaning of the previous results is as follows. If at least one of the two species is a weak competitor ($\alpha < 1$ or $\beta < 1$), then the system possesses only synchronized (homogeneous) stationary states: Either the first species is extinct in all patches, or the second species is extinct in all patches, or both species are extinct in all patches, or both species live in coexistence in all patches. In the opposite case when both species are strong competitors ($\alpha > 1$ and $\beta > 1$), there exist additional stationary states that are heterogeneous, i.e., with no synchronization between the patches: Some patches are dominated by the first species and the second species is close to extinction, some patches are dominated by the second species, and the remaining patches correspond to coexistence. Those heterogeneous states where at least one patch corresponds to coexistence (i.e., is close to S_3) are unstable, since S_3 is an unstable equilibrium of the non-diffusive system (2.11).

The following slightly more complicated example represents a model of three competing species.

Example 2.10. We consider the Lotka-Volterra system

$$\begin{aligned}
x'(t) &= \rho_1 x(t)(1 - x(t) - b_{12}y(t)),\\
y'(t) &= \rho_2 y(t)(1 - b_{21}x(t) - y(t) - b_{23}z(t)),\\
z'(t) &= \rho_3 z(t)(1 - b_{32}y(t) - z(t)),
\end{aligned}$$

where b_{12}, b_{21}, b_{23}, $b_{32} > 0$ are parameters. These equations correspond to the situation when there is a competition between species 1 and 2, and also between species 2 and 3. For example, there might be two different types of food: Species 1 eats only the first type, species 3 only the second type, while species 2 eats both types.

A diffusive version of this three species model was investigated in [2], [3], [4], [24], where the spatial domain is the set of all integers (i.e., the authors consider lattice differential equations). For a finite graph, we obtain the reaction-diffusion equations

$$\begin{aligned}
(x^i)'(t) &= \sum_{j\in\mathcal{N}(i)} d_1^{ij}(x^j(t) - x^i(t)) + \rho_1 x^i(t)(1 - x^i(t) - b_{12}y^i(t)), && i \in V(G),\\
(y^i)'(t) &= \sum_{j\in\mathcal{N}(i)} d_2^{ij}(y^j(t) - y^i(t)) + \rho_2 y^i(t)(1 - b_{21}x^i(t) - y^i(t) - b_{23}z^i(t)), && i \in V(G),\\
(z^i)'(t) &= \sum_{j\in\mathcal{N}(i)} d_3^{ij}(z^j(t) - z^i(t)) + \rho_3 z^i(t)(1 - b_{32}y^i(t) - z^i(t)), && i \in V(G).
\end{aligned} \tag{2.13}$$

Using a suitable software for symbolic calculations (we used *Wolfram Mathematica*), one finds that the equilibria are

$$S_0 = (0,0,0), \quad S_1 = (1,0,0), \quad S_2 = (0,1,0), \quad S_3 = (0,0,1), \quad S_4 = (1,0,1), \tag{2.14}$$

$$S_5 = \left(0, \frac{1-b_{23}}{1-b_{23}b_{32}}, \frac{1-b_{32}}{1-b_{23}b_{32}}\right), \quad S_6 = \left(\frac{1-b_{12}}{1-b_{12}b_{21}}, \frac{1-b_{21}}{1-b_{12}b_{21}}, 0\right), \tag{2.15}$$

$$S_7 = \frac{1}{1-b_{12}b_{21}-b_{23}b_{32}}\left(1-b_{12}+b_{12}b_{23}-b_{23}b_{32}, 1-b_{21}b_{23}, 1-b_{12}b_{21}-b_{32}+b_{21}b_{32}\right), \tag{2.16}$$

provided that the denominators of all fractions are nonzero (this will be satisfied in all cases that we consider below).

Depending on the values of the competition coefficients, some of the equilibria S_5, S_6, S_7 might have negative components. In particular, S_5 is nonnegative only if either $b_{23}, b_{32} < 1$, or $b_{23}, b_{32} > 1$. Similarly, S_6 is nonnegative only if either $b_{12}, b_{21} < 1$, or $b_{12}, b_{21} > 1$. The conditions for nonnegativity of S_7 are more complicated, and involve several cases to be considered. Instead of analyzing all possible values of the competition coefficients, we will consider only three representative cases. In each case, one can check that all relevant Jacobian determinants are nonzero:

$$\begin{aligned}
\det J_h(S_0) &= \rho_1\rho_2\rho_3,\\
\det J_h(S_1) &= \rho_1\rho_2\rho_3(b_{21}-1),\\
\det J_h(S_2) &= \rho_1\rho_2\rho_3(1-b_{12})(b_{32}-1),\\
\det J_h(S_3) &= \rho_1\rho_2\rho_3(b_{23}-1),\\
\det J_h(S_4) &= \rho_1\rho_2\rho_3(1-b_{21}-b_{23}),\\
\det J_h(S_5) &= \rho_1\rho_2\rho_3\frac{(b_{23}-1)(b_{32}-1)(1-b_{23}b_{32}+b_{12}b_{23}-b_{12})}{(b_{23}b_{32}-1)^2},\\
\det J_h(S_6) &= \rho_1\rho_2\rho_3\frac{(b_{12}-1)(b_{21}-1)(1-b_{12}b_{21}+b_{32}b_{21}-b_{32})}{(b_{12}b_{21}-1)^2},\\
\det J_h(S_7) &= \rho_1\rho_2\rho_3\frac{(b_{21}+b_{23}-1)(1-b_{12}b_{21}+b_{32}b_{21}-b_{32})(1-b_{23}b_{32}+b_{12}b_{23}-b_{12})}{(b_{12}b_{21}+b_{23}b_{32}-1)^2}.
\end{aligned}$$

In each of the following cases, our goal is to determine the maximal admissible sets for the system (2.13). According to Remark 2.8, we know that one maximal admissible set is $\mathcal{A}_1 = \{S_0\}$.

1. Case $b_{12} > 1$, $b_{32} > 1$, $b_{21} + b_{23} < 1$ (this case was considered in [3], [24]): The equilibria S_5, S_6, S_7 have some negative components. Hence, we have to find all maximal admissible sets contained in $\{S_1, S_2, S_3, S_4\}$. Consider $S_\sigma = (S_{\sigma(1)}, \dots, S_{\sigma(n)})$ with $\sigma(1), \dots, \sigma(n) \in \{1,2,3,4\}$, and choose an arbitrary $i \in V(G)$.

   If $\sigma(i) = 1$, then $u_2^i(0) = u_3^i(0) = 0$. Since $\frac{\partial h_2}{\partial y}(S_1) = \rho_2(1-b_{21}) > 0$ and $\frac{\partial h_3}{\partial z}(S_1) = \rho_3 > 0$, it follows from Theorem 2.2 that the continuation of S_σ is not nonnegative unless $u_2^j(0) = 0$ and $u_3^j(0) = 0$ for all $j \in V(G)$, which happens if only if $\sigma(j) = 1$ for all $j \in V(G)$.

   If $\sigma(i) = 3$, then $u_1^i(0) = u_2^i(0) = 0$. Since $\frac{\partial h_1}{\partial x}(S_3) = \rho_1 > 0$ and $\frac{\partial h_2}{\partial y}(S_3) = \rho_2(1-b_{23}) > 0$, it follows from Theorem 2.2 that the continuation of S_σ is not nonnegative unless $u_1^j(0) = 0$ and $u_2^j(0) = 0$ for all $j \in V(G)$, which happens if only if $\sigma(j) = 3$ for all $j \in V(G)$.

   If $\sigma(i) = 4$, then $u_2^i(0) = 0$. Since $\frac{\partial h_2}{\partial y}(S_4) = \rho_2(1-b_{21}-b_{23}) > 0$, it follows from Theorem 2.2 that the continuation of S_σ is not nonnegative unless $u_2^j(0) = 0$ for all $j \in V(G)$. Because the cases $\sigma(j) \in \{1,3\}$ were already ruled out, the only remaining possibility is $\sigma(j) = 4$ for all $j \in V(G)$.

   Our analysis shows that the maximal admissible sets are

   $$\mathcal{A}_1 = \{S_0\}, \quad \mathcal{A}_2 = \{S_1\}, \quad \mathcal{A}_3 = \{S_2\}, \quad \mathcal{A}_4 = \{S_3\}, \quad \mathcal{A}_5 = \{S_4\},$$

   which correspond only to homogeneous stationary states.

2. Case $b_{12} > 1$, $b_{32} > 1$, $b_{21} < 1$, $b_{23} < 1$, $b_{21} + b_{23} > 1$ (this case was considered in [2], [4]): The equilibria S_5, S_6 have some negative components, while S_7 has positive components. Hence, we have to find all maximal admissible sets contained in $\{S_1, S_2, S_3, S_4, S_7\}$. Consider $S_\sigma = (S_{\sigma(1)}, \dots, S_{\sigma(n)})$ with $\sigma(1), \dots, \sigma(n) \in \{1, 2, 3, 4, 7\}$, and choose an arbitrary $i \in V(G)$.

   As in the previous case, if $\sigma(i) = 1$ or $\sigma(i) = 3$, then the continuation of S_σ is nonnegative only if $\sigma(1) = \cdots = \sigma(n)$.

   If $\sigma(i) = 2$, then $u_1^i(0) = u_3^i(0) = 0$. Since $\frac{\partial h_1}{\partial x}(S_2) = \rho_1(1 - b_{12}) < 0$ and $\frac{\partial h_3}{\partial z}(S_2) = \rho_3(1 - b_{32}) < 0$, Theorem 2.2 yields no restrictions on the remaining values $\sigma(j)$.

   If $\sigma(i) = 4$, then $u_2^i(0) = 0$. Since $\frac{\partial h_2}{\partial y}(S_4) = \rho_2(1 - b_{21} - b_{23}) < 0$, Theorem 2.2 again yields no restrictions on the remaining values $\sigma(j)$.

   If $\sigma(i) = 7$, there is nothing to check because S_7 has positive components.

   Our analysis leads to the following maximal admissible sets:

$$\mathcal{A}_1 = \{S_0\}, \quad \mathcal{A}_2 = \{S_1\}, \quad \mathcal{A}_3 = \{S_3\}, \quad \mathcal{A}_4 = \{S_2, S_4, S_7\}.$$

   It follows that the system (2.13) with $d_k^{ij} = d\delta_k^{ij}$ has $3^n - 3$ nonnegative heterogeneous stationary states for all sufficiently small $d > 0$.

3. Case $b_{12} > 1$, $b_{32} > 1$, $b_{21} > 1$, $b_{23} > 1$: The equilibria S_5 and S_6 have nonnegative components. The fraction in the definition of S_7 given in (2.16) is negative, and therefore S_7 has positive components if and only if $1 - b_{12} + b_{12}b_{23} - b_{23}b_{32} < 0$ and $1 - b_{12}b_{21} - b_{32} + b_{21}b_{32} < 0$. Expressing these conditions in terms of b_{32}, we get

$$\frac{1 - b_{12} + b_{12}b_{23}}{b_{23}} < b_{32} < \frac{1 - b_{12}b_{21}}{1 - b_{21}}. \tag{2.17}$$

   Let us suppose that these conditions hold (for example, this happens for $b_{12} = b_{21} = \frac{3}{2}$ and $b_{23} = b_{32} = 2$).

   Our goal now is to find all maximal admissible sets contained in $\{S_1, S_2, S_3, S_4, S_5, S_6, S_7\}$. Consider $S_\sigma = (S_{\sigma(1)}, \dots, S_{\sigma(n)})$ with $\sigma(1), \dots, \sigma(n) \in \{1, 2, 3, 4, 5, 6, 7\}$, and choose an arbitrary $i \in V(G)$.

   If $\sigma(i) = 1$, then $u_2^i(0) = u_3^i(0) = 0$. Since $\frac{\partial h_2}{\partial y}(S_1) = \rho_2(1 - b_{21}) < 0$ and $\frac{\partial h_3}{\partial z}(S_1) = \rho_3 > 0$, it follows from Theorem 2.2 that the continuation of S_σ is not nonnegative unless $u_3^j(0) = 0$ for all $j \in V(G)$, which happens if only if $\sigma(j) \in \{1, 2, 6\}$ for all $j \in V(G)$.

   If $\sigma(i) = 3$, then $u_1^i(0) = u_2^i(0) = 0$. Since $\frac{\partial h_1}{\partial x}(S_3) = \rho_1 > 0$ and $\frac{\partial h_2}{\partial y}(S_3) = \rho_2(1 - b_{23}) < 0$, it follows from Theorem 2.2 that the continuation of S_σ is not nonnegative unless $u_1^j(0) = 0$ for all $j \in V(G)$, which happens if only if $\sigma(j) \in \{2, 3, 5\}$ for all $j \in V(G)$.

   As in the previous case, if $\sigma(i) = 2$ and $\sigma(i) = 4$, then the corresponding partial derivatives are negative, and Theorem 2.2 yields no restrictions on the remaining values $\sigma(j)$.

   If $\sigma(i) = 5$, then $u_1^i(0) = 0$. We have

$$\frac{\partial h_1}{\partial x}(S_5) = \rho_1 \left(1 + \frac{b_{12}(b_{23} - 1)}{1 - b_{23}b_{32}}\right) = \rho_1 \frac{1 - b_{23}b_{32} + b_{12}b_{23} - b_{12}}{1 - b_{23}b_{32}}.$$

   The denominator is negative, and the numerator is also negative by the first inequality in (2.17). Thus, since $\frac{\partial h_1}{\partial x}(S_5) > 0$, it follows from Theorem 2.2 that the continuation of S_σ is not nonnegative unless $u_1^j(0) = 0$ for all $j \in V(G)$, which happens if only if $\sigma(j) \in \{2, 3, 5\}$ for all $j \in V(G)$.

   If $\sigma(i) = 6$, then $u_3^i(0) = 0$. We have

$$\frac{\partial h_3}{\partial z}(S_6) = \rho_3 \left(1 + \frac{b_{32}(b_{21} - 1)}{1 - b_{12}b_{21}}\right) = \frac{1 - b_{12}b_{21} + b_{32}b_{21} - b_{32}}{1 - b_{12}b_{21}}.$$

   The denominator is negative, and the numerator is also negative by the second inequality in (2.17). Thus, since $\frac{\partial h_3}{\partial z}(S_6) > 0$, it follows from Theorem 2.2 that the continuation of S_σ is not nonnegative unless $u_3^j(0) = 0$ for all $j \in V(G)$, which happens if only if $\sigma(j) \in \{1, 2, 6\}$ for all $j \in V(G)$.

If $\sigma(i) = 7$, there is nothing to check because S_7 has positive components.

Our analysis leads to the following maximal admissible sets:

$$\mathcal{A}_1 = \{S_0\}, \quad \mathcal{A}_2 = \{S_1, S_2, S_6\}, \quad \mathcal{A}_3 = \{S_2, S_3, S_5\}, \quad \mathcal{A}_4 = \{S_2, S_4, S_7\}.$$

These sets are not pairwise disjoint, but the intersection of any two has at most one element. By the formula (2.7), the system (2.13) with $d_k^{ij} = d\delta_k^{ij}$ has $3(3^n - 3)$ nonnegative heterogeneous stationary states for all sufficiently small $d > 0$.

Biological interpretation. The biological meaning is as follows. In case 1, the second species is a strong competitor, while the first and third species are weak. In this case, the system possesses only synchronized stationary states. In case 2, the first and third species are still weak, but their collective influence on the second species is no longer negligible. The system has heterogeneous stationary states, where some patches are dominated by the second species (and the first and third species are close to extinction), some patches are dominated by the first and third species (their populations being almost identical), and the remaining patches correspond to coexistence of all three species. In case 3, all species are strong competitors, and the system possesses three types of heterogeneous stationary states: In the first type, the third species is extinct in all patches; each patch is dominated by the first species, or by the second species, or corresponds to their coexistence. Similarly, in the second type, the first species is extinct in all patches; each patch is dominated by the second species, or by the third species, or corresponds to their coexistence. In the third type, each patch is either dominated by the second species (and the first and third species are close to extinction), or by the first and third species (their populations being almost identical), or it corresponds to coexistence of all three species.

The next examples show the applicability of Theorem 2.2 to systems that are not of Lotka-Volterra type.

Example 2.11. The following model describing the competition between two species subject to an Allee effect was introduced in [23]:

$$\begin{aligned} x'(t) &= x(t)\left(b_1\left(1 - \frac{x(t) + \alpha y(t)}{r_1}\right)\left(\frac{x(t)}{x(t) + c_1}\right) - d_1\right), \\ y'(t) &= y(t)\left(b_2\left(1 - \frac{y(t) + \beta x(t)}{r_2}\right)\left(\frac{y(t)}{y(t) + c_2}\right) - d_2\right). \end{aligned} \tag{2.18}$$

For $c_1 = c_2 = 0$, the system reduces to the classical Lotka-Volterra competition model. Here we assume that both c_1 and c_2 are positive, which means that each population is subject to a strong Allee effect, i.e., it has a critical population size under which the population growth rate is negative.

The corresponding reaction-diffusion equations are

$$\begin{aligned} (x^i)'(t) &= \sum_{j \in \mathcal{N}(i)} d_1^{ij}(x^j(t) - x^i(t)) + x^i(t)\left(b_1\left(1 - \frac{x^i(t) + \alpha y^i(t)}{r_1}\right)\left(\frac{x^i(t)}{x^i(t) + c_1}\right) - d_1\right), \qquad i \in V(G), \\ (y^i)'(t) &= \sum_{j \in \mathcal{N}(i)} d_2^{ij}(y^j(t) - y^i(t)) + y^i(t)\left(b_2\left(1 - \frac{y^i(t) + \beta x^i(t)}{r_2}\right)\left(\frac{y^i(t)}{y^i(t) + c_2}\right) - d_2\right), \qquad i \in V(G). \end{aligned} \tag{2.19}$$

Note that $h_1(x, y) = x\left(b_1\left(1 - \frac{x+\alpha y}{r_1}\right)\left(\frac{x}{x+c_1}\right) - d_1\right)$ and $h_2(x, y) = y\left(b_2\left(1 - \frac{y+\beta x}{r_2}\right)\left(\frac{y}{y+c_2}\right) - d_2\right)$ are real analytic in $[0, \infty) \times [0, \infty)$, since a rational function is analytic at all points where its denominator is nonzero.

For certain values of the parameters b_1, b_2, r_1, r_2, α, β, c_1, c_2, d_1, d_2, which are assumed to be positive, the system (2.18) has nine nonnegative equilibrium points: the extinction state $S_1 = (0, 0)$, two equilibria S_2 and S_3 on the positive x-semiaxis, two equilibria S_4 and S_5 on the positive y-semiaxis, and four coexistence equilibria S_6, S_7, S_8, S_9; see the left part of Figure 1. The coordinates of all equilibria can be calculated analytically, but they are unimportant for our purposes. Let us also assume that all equilibria are hyperbolic; for particular values of the parameters, one can verify this fact by numerical calculation.

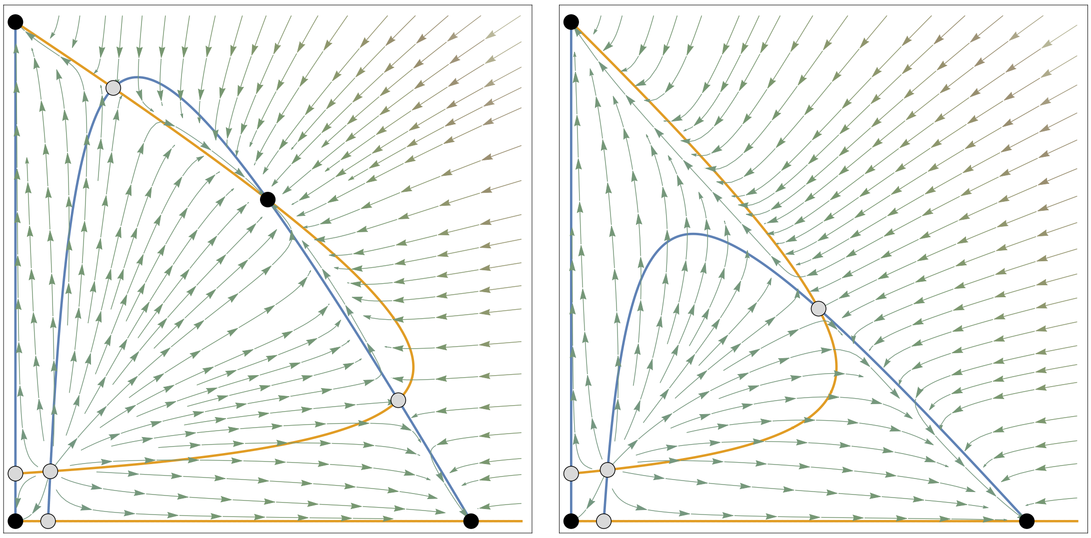

Figure 1: Phase portraits of the system (2.18). The colored curves are the nullclines $h_1(x, y) = 0$ and $h_2(x, y) = 0$, the black/gray points are stable/unstable equilibria. The left figure corresponds to $b_1 = 0.11$, $\alpha = 0.55$, $r_1 = 45$, $c_1 = 12$, $d_1 = 0.018$, $b_2 = 0.09$, $\beta = 0.6$, $r_2 = 55$, $c_2 = 11$, $d_2 = 0.021$. The right figure corresponds to $b_1 = 0.11$, $\alpha = 0.85$, $r_1 = 45$, $c_1 = 12$, $d_1 = 0.018$, $b_2 = 0.09$, $\beta = 0.9$, $r_2 = 55$, $c_2 = 11$, $d_2 = 0.021$. These parameter values are taken from [23].

Next, we calculate

$$\frac{\partial h_1}{\partial y}(x,y) = -\frac{\alpha b_1 x^2}{r_1(c_1+x)}, \quad \frac{\partial h_2}{\partial x}(x,y) = -\frac{\beta b_2 y^2}{r_2(c_2+y)},$$
$$\frac{\partial^j h_1}{\partial y^j}(x,y) = 0, \quad \frac{\partial^j h_2}{\partial x^j}(x,y) = 0 \text{ for } j \in \{2,3,4,\dots\}.$$

Hence, if $x = 0$, then $\frac{\partial^j h_1}{\partial y^j}(x, y) = 0$ for all $j \in \mathbb{N}$, and if $y = 0$, then $\frac{\partial^j h_2}{\partial x^j}(x, y) = 0$ for all $j \in \mathbb{N}$, showing that the assumptions of Theorem 2.2 are satisfied with $\Sigma = \{S_1, \dots, S_9\}$.

Let $S_\sigma = (S_{\sigma(1)}, \dots, S_{\sigma(n)})$, where $\sigma(1), \dots, \sigma(n) \in \{1, \dots, 9\}$, and choose an arbitrary $i \in V(G)$. To see whether the continuation of S_σ is nonnegative for $d_k^{ij} = d\delta_k^{ij}$ and small $d > 0$, we need to check only situations where $S_{\sigma(i)}$ has a zero component.

If $u_1^i(0) = 0$, then $\frac{\partial h_1}{\partial x}(S_{\sigma(i)}) = \frac{\partial h_1}{\partial x}(0, u_2^i(0)) = -d_1 < 0$, and Theorem 2.2 yields no restrictions on the remaining values $\sigma(j)$. Similarly, if $u_2^i(0) = 0$, then $\frac{\partial h_2}{\partial y}(S_{\sigma(i)}) = \frac{\partial h_2}{\partial y}(u_1^i(0), 0) = -d_2 < 0$, and again we get no restrictions on the remaining values $\sigma(j)$.

Consequently, we have one maximal admissible set $\mathcal{A}_1 = \{S_1, \dots, S_9\}$, and therefore the system (2.19) with $d_k^{ij} = d\delta_k^{ij}$ has $9^n - 9$ nonnegative heterogeneous stationary states for all sufficiently small $d > 0$. According to Remark 2.5 and Figure 1, $4^n - 4$ of them are locally asymptotically stable.

Note that for other choices of the parameters, the system (2.18) might have less than four coexistence equilibria. In general, if the set Σ consists of s nonnegative equilibria, the previous calculation shows that the system (2.19) with $d_k^{ij} = d\delta_k^{ij}$ has $s^n - s$ nonnegative heterogeneous stationary states for all sufficiently small $d > 0$. For example, the right part of Figure 1 depicts a situation with only two coexistence equilibria S_6, S_7; the corresponding reaction-diffusion equation has $7^n - 7$ nonnegative heterogeneous stationary states for small $d > 0$; $3^n - 3$ of them are locally asymptotically stable.

Biological interpretation. The biological meaning is similar as in the case of the two-species Lotka-Volterra competition model (Example 2.9): For suitable values of the parameters, there exist heterogeneous stationary states with no synchronization among the patches. Some patches are dominated by the first species, other by the second species, and there is coexistence in the remaining patches. However, there is an important difference in comparison with the two-species Lotka-Volterra model: The heterogeneous states where some patches correspond to coexistence might be stable; see the left part of Figure 1, where one of the coexistence equilibria is stable.

In the previous example, all equilibria obtained by continuation from the implicit function theorem were nonnegative. The next example represents an opposite extreme.

Example 2.12. The Gause predator-prey model has the form (see [1, Chapter 4])

$$\begin{aligned} x'(t) &= x(t)g(x(t)) - y(t)p(x(t)), \\ y'(t) &= y(t)(-\delta + q(x(t))). \end{aligned} \tag{2.20}$$

The constant $\delta > 0$ is the death rate for the predator. The function g corresponds to the specific growth rate for the prey; we assume that $g' < 0$ on $(0, \infty)$, and there exists a $K > 0$ (carrying capacity for the prey) such that $g > 0$ on $[0, K)$, $g(K) = 0$, $g < 0$ on (K, ∞). The function p describes the number of prey eaten by each predator; we assume that $p(0) = 0$ and $p > 0$ on $(0, \infty)$. Finally, the function q gives the effectiveness of the prey consumption by predators; we assume that $q(0) = 0$, $q > 0$ on $(0, \infty)$ and $q' > 0$ on $(0, \infty)$. For example, these assumptions are satisfied if $g(x) = \alpha(1 - \frac{x}{K})$, and $p(x) = q(x) = \frac{\beta x}{x+\gamma}$ (Holling type II response corresponding to predator satiation) with $\alpha, \beta, \gamma, K > 0$.

The corresponding reaction-diffusion equations are

$$\begin{aligned} (x^i)'(t) &= \sum_{j \in \mathcal{N}(i)} d_1^{ij}(x^j(t) - x^i(t)) + x^i(t)g(x^i(t)) - y^i(t)p(x^i(t)), \qquad && i \in V(G), \\ (y^i)'(t) &= \sum_{j \in \mathcal{N}(i)} d_2^{ij}(y^j(t) - y^i(t)) + y^i(t)(-\delta + q(x^i(t))), && i \in V(G). \end{aligned} \tag{2.21}$$

The system (2.20) always has at least two equilibria, $S_1 = (0, 0)$ and $S_2 = (K, 0)$. If there exists an $x_0 > 0$ such that $q(x_0) = \delta$, we get a third equilibrium $S_3 = (x_0, \frac{x_0 g(x_0)}{p(x_0)})$. This equilibrium has positive components if $x_0 < K$; for this moment, let us assume only that $x_0 \neq K$, and therefore $q(K) \neq \delta$. To be able to use Theorem 2.2, suppose that g, p, q are real analytic at 0, x_0, K; then the reaction functions $h_1(x, y) = xg(x) - yp(x)$ and $h_2(x, y) = y(-\delta + q(x))$ are real analytic at S_1, S_2, S_3. (In the above-mentioned example with Holling type II response, both p and q are quotients of real analytic functions, and therefore real analytic at all points except $x = -\gamma$ where the denominator vanishes.)

The Jacobian matrix is

$$J_h(x, y) = \begin{pmatrix} g(x) + xg'(x) - yp'(x) & -p(x) \\ yq'(x) & -\delta + q(x) \end{pmatrix},$$

and it is easily seen that our assumptions on g, p, q guarantee that

$$J_h(S_1) = \begin{pmatrix} g(0) & 0 \\ 0 & -\delta \end{pmatrix}, \quad J_h(S_2) = \begin{pmatrix} Kg'(K) & -p(K) \\ 0 & -\delta + q(K) \end{pmatrix}, \quad J_h(S_3) = \begin{pmatrix} \cdots & -p(x_0) \\ \frac{x_0 g(x_0)}{p(x_0)} q'(x_0) & 0 \end{pmatrix}$$

are all invertible (dots correspond to terms whose value is unimportant). To check that Theorem 2.2 is applicable, we observe that if $x = 0$, then $\frac{\partial h_1}{\partial y}(x, y) = -p(x) = 0$, $\frac{\partial^k h_1}{\partial y^k}(x, y) = 0$ for all $k \geq 2$, and if $y = 0$, then $\frac{\partial^k h_2}{\partial x^k}(x, y) = yq^{(k)}(x) = 0$ for all $k \geq 1$.

Let $S_\sigma = (S_{\sigma(1)}, \ldots, S_{\sigma(n)})$, where $\sigma(1), \ldots, \sigma(n) \in \{1, 2, 3\}$, and choose an arbitrary $i \in V(G)$. To see whether the continuation of S_σ is nonnegative for small $d > 0$, we need to check only situations where $S_{\sigma(i)}$ has a zero component, i.e., $\sigma(i) \in \{1, 2\}$.

If $\sigma(i) = 1$, then $u_1^i(0) = u_2^i(0) = 0$. We have $\frac{\partial h_1}{\partial x}(S_1) = g(0) > 0$ and $\frac{\partial h_2}{\partial y}(S_1) = -\delta < 0$. Hence, Theorem 2.2 requires $u_1^j(0) = 0$ for all $j \in V(G)$, which happens only if $\sigma(j) = 1$ for all $j \in V(G)$.

If $\sigma(i) = 2$, then $u_2^i(0) = 0$, and $\frac{\partial h_2}{\partial y}(S_2) = -\delta + q(K)$. If $K > x_0$, then $\frac{\partial h_2}{\partial y}(S_2) > 0$, and Theorem 2.2 requires $u_2^j(0) = 0$ for all $j \in V(G)$, which happens only if $\sigma(j) \in \{1, 2\}$ for all $j \in V(G)$. If $K < x_0$, then

$\frac{\partial h_2}{\partial y}(S_2) < 0$ and there are no restrictions on the remaining values $\sigma(j)$, but in this case S_3 does not have nonnegative components.

The previous analysis shows that the maximal admissible sets are $\mathcal{A}_1 = \{S_1\}$, $\mathcal{A}_2 = \{S_2\}$, and $\mathcal{A}_3 = \{S_3\}$ if $K > x_0$. In any case, we get only homogeneous stationary states.[1]

Biological interpretation. The biological meaning is clear: No matter what are the values of K and x_0, the system has only synchronized stationary states: Either both species are extinct in all patches, or the prey survives and the predator dies out in all patches, or they live in coexistence in all patches.

Let us remark that a similar analysis can be performed for other predator-prey models, such as the Beddington–DeAngelis predator-prey model described in [5]; again, it turns out that the diffusive version has no nonnegative heterogeneous stationary states for small $d > 0$.

3 Lyapunov functions

We turn our attention to the second problem mentioned in the introduction: Given a Lyapunov function V for the non-diffusive system (1.1), we are interested in finding a Lyapunov function W for the diffusive system (1.2). The next result is applicable in the case when we have symmetric diffusion and the Lyapunov function V is a sum of univariate functions with nondecreasing derivatives.

Theorem 3.1. *Assume that $d_k^{ij} = d_k^{ji}$ whenever $\{i,j\} \in E(G)$ and $k \in \{1,\dots,N\}$. Suppose also that for each $k \in \{1,\dots,N\}$, $I_k \subset \mathbb{R}$ is an interval and $V_k : I_k \to \mathbb{R}$ has a nondecreasing derivative. Let $M = I_1 \times \cdots \times I_N \subset \mathbb{R}^N$ and*

$$V(x) = V_1(x_1) + \cdots + V_N(x_N), \quad x \in M.$$

Let $W : M^n \to \mathbb{R}$ be given by

$$W(x^1,\dots,x^n) = V(x^1) + \cdots + V(x^n) = \sum_{i \in V(G)} \sum_{k=1}^{N} V_k(x_k^i).$$

Then the following statements hold:

1. *If $\dot V \le 0$ in M, i.e., V has nonpositive orbital derivative with respect to the system* (1.1) *in M, then $\dot W \le 0$ in M^n, i.e., W has nonpositive orbital derivative with respect to the system* (1.2) *in M^n.*
2. *If $\dot W(x^1,\dots,x^n) = 0$, then the following conditions hold:*
   - *$\dot V(x_1^i,\dots,x_N^i) = 0$ for each $i \in V(G)$.*
   - *If $k \in \{1,\dots,N\}$ is such that V_k' is increasing on I_k, then $x_k^1 = \cdots = x_k^n$.*
3. *If V_k' is increasing on I_k for each $k \in \{1,\dots,N\}$, $(x^1,\dots,x^n) \in M^n$ is such that $\dot V(x_1^i,\dots,x_N^i) = 0$ for each $i \in V(G)$, and $x_k^1 = \cdots = x_k^n$ for each $k \in \{1,\dots,N\}$, then $\dot W(x^1,\dots,x^n) = 0$.*

Proof. The orbital derivative of W with respect to (1.2) is

$$\dot W(x^1,\dots,x^n) = \sum_{i \in V(G)} \sum_{k=1}^{N} \frac{\partial W}{\partial x_k^i}(x^1,\dots,x^n) \left(\sum_{j \in \mathcal{N}(i)} d_k^{ij}(x_k^j - x_k^i) + h_k(x_1^i,\dots,x_N^i) \right)$$
$$= \sum_{i \in V(G)} \sum_{k=1}^{N} \frac{\partial V}{\partial x_k}(x_1^i,\dots,x_N^i) \left(\sum_{j \in \mathcal{N}(i)} d_k^{ij}(x_k^j - x_k^i) + h_k(x_1^i,\dots,x_N^i) \right)$$
$$= \sum_{i \in V(G)} \sum_{k=1}^{N} \sum_{j \in \mathcal{N}(i)} d_k^{ij} \frac{\partial V}{\partial x_k}(x_1^i,\dots,x_N^i)(x_k^j - x_k^i) + \sum_{i \in V(G)} \sum_{k=1}^{N} \frac{\partial V}{\partial x_k}(x_1^i,\dots,x_N^i) h_k(x_1^i,\dots,x_N^i).$$

[1] An inspection of the previous calculation shows that the assumptions on g and q can be somewhat weakened: Instead of requiring $g' < 0$ on $(0,\infty)$, it suffices to assume $g'(K) < 0$. Also, instead of requiring $q' > 0$ on $(0,\infty)$, it is enough to suppose that q is strictly increasing on $[0,\infty)$, and $q'(x_0) > 0$.

The inner term in the second sum is the orbital derivative $\dot{V}(x_1^i, \dots, x_N^i)$ with respect to the system (1.1), which is assumed to be nonpositive. Thus, we get the estimate

$$\dot{W}(x^1, \dots, x^n) \le \sum_{k=1}^{N} \sum_{i \in V(G)} \sum_{j \in \mathcal{N}(i)} d_k^{ij} \frac{\partial V}{\partial x_k}(x_1^i, \dots, x_N^i)(x_k^j - x_k^i) = \sum_{k=1}^{N} \sum_{i \in V(G)} \sum_{j \in \mathcal{N}(i)} d_k^{ij} V_k'(x_k^i)(x_k^j - x_k^i).$$

Using the fact that $d_k^{ij} = d_k^{ji}$, we further obtain

$$\begin{aligned} \dot{W}(x^1, \dots, x^n) &\le \sum_{k=1}^{N} \sum_{\{i,j\} \in E(G)} d_k^{ij} \left(V_k'(x_k^i)(x_k^j - x_k^i) + V_k'(x_k^j)(x_k^i - x_k^j) \right) \\ &= \sum_{k=1}^{N} \sum_{\{i,j\} \in E(G)} d_k^{ij} (x_k^j - x_k^i) \left(V_k'(x_k^i) - V_k'(x_k^j) \right) \le 0, \end{aligned}$$

since the terms $x_k^j - x_k^i$ and $V_k'(x_k^i) - V_k'(x_k^j)$ either both vanish or have opposite signs because V_k' is nondecreasing.

If $\dot{W}(x^1, \dots, x^n) = 0$, an inspection of the previous proof shows that $\dot{V}(x_1^i, \dots, x_N^i) = 0$ for each $i \in V(G)$, and if V_k' is increasing, then $x_k^j = x_k^i$ whenever $\{i, j\} \in E(G)$. However, since the graph is connected, the latter condition implies $x_k^1 = \cdots = x_k^n$.

Clearly, if all the derivatives V_k' are increasing, then the previous conditions are also sufficient for the orbital derivative of W to vanish. □

Lyapunov functions are useful for proving global stability of an equilibrium point. In this situation, the equilibrium has to be a strict global minimum of the Lyapunov function. Suppose that the assumptions of Theorem 3.1 hold. If each univariate function V_k has a strict local minimum at $x_k^* \in I_k$, then V has a strict local minimum at $(x_1^*, \dots, x_N^*) \in M$, and W has a strict local minimum at $(x^1, \dots, x^n) \in M^n$, where $x^i = (x_1^*, \dots, x_N^*)$ for each $i \in V(G)$. This observation will be used without further comments.

In the following examples, we use Theorem 3.1 to demonstrate global stability of homogeneous stationary states for various systems; note that this fact rules out the existence of heterogeneous stationary states no matter whether the diffusion is small or large.

Example 3.2 (SIR epidemic model)**.** The well-known SIR (susceptible-infectious-removed) epidemic model (with vital dynamics and constant population) has the form

$$S'(t) = \gamma - \beta S(t)I(t) - \sigma S(t), \quad I'(t) = \beta S(t)I(t) - \delta I(t), \tag{3.1}$$

where all parameters are positive. A differential equation for the removed class is omitted, since the total population remains constant. The dynamics of this model depends on the number $R_0 = \frac{\beta\gamma}{\sigma\delta}$, called the basic reproduction number.

If $R_0 < 1$, then the only nonnegative equilibrium is the disease-free equilibrium $(S_0^*, I_0^*) = (\frac{\gamma}{\sigma}, 0)$. It is globally asymptotically stable in $M = (0, \infty) \times [0, \infty)$; this follows (see [12, Remark 3]) from the existence of the Lyapunov function

$$V(S, I) = S_0^* \left(\frac{S}{S_0^*} - \ln \frac{S}{S_0^*} \right) + I, \quad (S, I) \in M, \tag{3.2}$$

which attains its global minimum in (S_0^*, I_0^*), and has nonpositive orbital derivative

$$\dot{V}(S, I) = -\gamma \frac{S_0^*}{S} \left(1 - \frac{S}{S_0^*} \right)^2 - \delta(1 - R_0)I,$$

which vanishes only for $(S, I) = (S_0^*, I_0^*)$.

If $R_0 > 1$, there is a second positive equilibrium

$$(S_1^*, I_1^*) = \left(\frac{\delta}{\beta}, \frac{\gamma}{\delta} - \frac{\sigma}{\beta} \right) = \left(\frac{\gamma}{\delta R_0}, \frac{\gamma}{\delta} \left(1 - \frac{1}{R_0} \right) \right),$$

called the endemic equilibrium. It is globally asymptotically stable in $(0,\infty)^2$; this follows (see [12, Theorem 1]) from the existence of the Lyapunov function

$$V(S,I) = S_1^*\left(\frac{S}{S_1^*} - \ln\frac{S}{S_1^*}\right) + I_1^*\left(\frac{I}{I_1^*} - \ln\frac{I}{I_1^*}\right), \quad (S,I) \in (0,\infty)^2, \tag{3.3}$$

which attains its global minimum in (S_1^*, I_1^*), and has nonpositive orbital derivative

$$\dot{V}(S,I) = -\gamma\frac{S_1^*}{S}\left(1 - \frac{S}{S_1^*}\right)^2,$$

which vanishes if and only if $S = S_1^*$.

The diffusive SIR epidemic model obtained from (3.1) has the form

$$(S^i)'(t) = \sum_{j\in\mathcal{N}(i)} d_1^{ij}(S^j(t) - S^i(t)) + \gamma - \beta S^i(t)I^i(t) - \sigma S^i(t), \quad i \in V(G), \tag{3.4}$$

$$(I^i)'(t) = \sum_{j\in\mathcal{N}(i)} d_2^{ij}(I^j(t) - I^i(t)) + \beta S^i(t)I^i(t) - \delta I^i(t), \quad i \in V(G), \tag{3.5}$$

and it is a special case of (1.2) with $N = 2$.

The Lyapunov function in (3.2) has the form $V(S,I) = V_1(S) + V_2(I)$, where $V_1(S) = S_0^*\left(\frac{S}{S_0^*} - \ln\frac{S}{S_0^*}\right)$ and $V_2(I) = I$. Note that V_1' is increasing on $(0,\infty)$ and V_2' is constant on $[0,\infty)$. If $R_0 < 1$, then $\dot{V} \le 0$ in $(0,\infty)\times[0,\infty)$ and V satisfies the assumptions of Theorem 3.1. Hence, the function

$$W(S^1, I^1, \dots, S^n, I^n) = \sum_{i\in V(G)} V(S^i, I^i) \tag{3.6}$$

satisfies $\dot{W} \le 0$ in $((0,\infty)\times[0,\infty))^n$. If $\dot{W} = 0$, then the second part of Theorem 3.1 implies $\dot{V}(S^i, I^i) = 0$ for every $i \in V(G)$, and therefore $(S^i, I^i) = (S_0^*, I_0^*)$ for every $i \in V(G)$. Consequently, if $R_0 < 1$, this homogeneous disease-free equilibrium is globally asymptotically stable in $((0,\infty)\times[0,\infty))^n$.

The Lyapunov function in (3.3) has the form $V(S,I) = V_1(S) + V_2(I)$, where $V_1(S) = S_1^*\left(\frac{S}{S_1^*} - \ln\frac{S}{S_1^*}\right)$ and $V_2(I) = I_1^*\left(\frac{I}{I_1^*} - \ln\frac{I}{I_1^*}\right)$. Note that V_1' and V_2' are increasing on $(0,\infty)$. If $R_0 > 1$, then $\dot{V} \le 0$ in $(0,\infty)^2$ and V satisfies the assumptions of Theorem 3.1. Hence, the function (3.6) satisfies $\dot{W} \le 0$ in $(0,\infty)^{2n}$. According to the second and third part of Theorem 3.1, the equality $\dot{W} = 0$ holds if and only if $\dot{V}(S^i, I^i) = 0$ for every $i \in V(G)$, $S^1 = \dots = S^n$ and $I^1 = \dots = I^n$. From the first equality, we get $S^1 = \dots = S^n = S_1^*$. The only invariant subset of the set

$$\{(S^1, I^1, \dots, S^n, I^n) \in M^n : \dot{W}(S^1, I^1, \dots, S^n, I^n) = 0\}$$

is the singleton set $\{(S_1^*, I_1^*, \dots, S_1^*, I_1^*)\}$. Indeed, if $S^1(t) = \dots = S^n(t) = S_1^* = \frac{\delta}{\beta}$ and $I^1(t) = \dots = I^n(t) \ne I_1^* = \frac{\gamma}{\delta} - \frac{\sigma}{\beta}$, then (3.4)–(3.5) imply

$$\begin{aligned}
(S^i)'(t) &= \gamma - \beta S_1^* I^i(t) - \sigma S_1^* = \gamma - \delta I^i(t) - \sigma\frac{\delta}{\beta} \ne 0, \quad i \in V(G),\\
(I^i)'(t) &= \beta S_1^* I^i(t) - \delta I^i(t) = 0, \quad i \in V(G),
\end{aligned}$$

and therefore $S^i(t) \ne S_1^*$ on a right neighborhood of t. Consequently, if $R_0 > 1$, LaSalle's invariance principle implies that the homogeneous endemic equilibrium with $(S^i, I^i) = (S_1^*, I_1^*)$ for all $i \in V(G)$ is globally asymptotically stable in $(0,\infty)^{2n}$.

Our results generalize those from the paper [21], which deals with global stability of the diffusive SIR epidemic model (3.4)–(3.5) in the case when $d_1^{ij} = d_2^{ij}$ for all $\{i,j\} \in E$, i.e., when the diffusion rates for the susceptible and infected populations coincide. For $R_0 > 1$, the authors used the Lyapunov function (3.3), but their analysis for $R_0 < 1$ does not rely on Lyapunov functions, and seems more complicated.

On the other hand, we do not suppose that the two diffusion rates coincide, and our treatment for both $R_0 < 1$ and $R_0 > 1$ relies on the Lyapunov functions presented in [12].

In a similar way, one can analyze the diffusive SIS (susceptible-infectious-susceptible) epidemic model. Again, it suffices to take the Lyapunov function for the non-diffusive model given in [12, Section 3], and use Theorem 3.1 to obtain a Lyapunov function for the diffusive model. The Lyapunov function is of the same type as in (3.3), i.e., a sum of linear terms with positive coefficients and logarithmic terms with negative coefficients; hence, the derivatives are increasing, and the assumptions of Theorem 3.1 are satisifed.

Example 3.3 (SEIR epidemic model with nonlinear incidence rate)**.** The SEIR (susceptible-exposed-infectious-removed) epidemic model with nonlinear incidence rate has the form

$$S'(t) = b - \beta S(t)^q I(t)^p - \mu S(t), \quad E'(t) = \beta S(t)^q I(t)^p - \sigma E(t), \quad I'(t) = \theta E(t) - \delta I(t),$$

where all parameters are positive. For more details on this model and the meaning of the parameters, see e.g. [11, 15]. A differential equation for the removed class is omitted, since the total population remains constant. Let us assume that $0 < p < 1$; in this case, it is known that the system has exactly two nonegative equilibria, the disease-free equilibrium $(S_0^*, E_0^*, I_0^*) = (\frac{b}{\mu}, 0, 0)$, and the endemic equlibrium (S_1^*, E_1^*, I_1^*), whose components represent the unique positive solution of the system

$$b = \beta S^q I^p + \mu S, \quad \beta S^q I^p = \sigma E, \quad \theta E = \delta I$$

(note that $E = \frac{\delta}{\theta} I$; substituting into the second equation, we get $I = (\frac{\beta\theta}{\sigma\delta} S^q)^{1/(1-p)}$; substituting into the first equation, we obtain a transcendental equation for S, which has a unique positive solution).

It was shown in [11] that if $p < 1$, then the endemic equilibrium is globally asympotically stable in $(0, \infty)^3$. The proof is based on the Lyapunov function

$$V(S, E, I) = S + E - E_1^* \ln E + \frac{(S_1^*)^q}{q-1} S^{1-q} + \frac{\sigma}{\theta}\left(I + \frac{(I_1^*)^p}{p-1} I^{1-p}\right), \quad S, E, I \in (0, \infty),$$

whose orbital derivative is nonpositive and vanishes only in (S_1^*, E_1^*, I_1^*). We have the decomposition $V(S, E, I) = V_1(S) + V_2(E) + V_3(I)$, where

$$V_1(S) = S + \frac{(S_1^*)^q}{q-1} S^{1-q}, \quad V_2(E) = E - E_1^* \ln E, \quad V_3(I) = \frac{\sigma}{\theta}\left(I + \frac{(I_1^*)^p}{p-1} I^{1-p}\right),$$
$$V_1'(S) = 1 - \left(\frac{S_1^*}{S}\right)^q, \quad V_2'(E) = 1 - \frac{E_1^*}{E}, \quad V_3'(I) = \frac{\sigma}{\theta}\left(1 - \left(\frac{I_1^*}{I}\right)^p\right).$$

The derivatives are increasing on $(0, \infty)$, and therefore the assumptions of Theorem 3.1 are satisfied. Hence, we get the Lyapunov function

$$W(S^1, E^1, I^1, \dots, S^n, E^n, I^n) = \sum_{i \in V(G)} V(S^i, E^i, I^i)$$

for the diffusive SEIR model

$$S_i'(t) = \sum_{j \in \mathcal{N}(i)} d_1^{ij}(S^j(t) - S^i(t)) + b - \beta S_i(t)^q I_i(t)^p - \mu S_i(t), \quad i \in V(G),$$
$$E_i'(t) = \sum_{j \in \mathcal{N}(i)} d_2^{ij}(E^j(t) - E^i(t)) + \beta S_i(t)^q I_i(t)^p - \sigma E_i(t), \quad i \in V(G),$$
$$I_i'(t) = \sum_{j \in \mathcal{N}(i)} d_3^{ij}(I^j(t) - I^i(t)) + \theta E_i(t) - \delta I_i(t), \quad i \in V(G).$$

According to Theorem 3.1, the orbital derivative of W is nonpositive in $(0, \infty)^{3n}$, and vanishes only if $(S^i, E^i, I^i) = (S_1^*, E_1^*, I_1^*)$ for every $i \in V(G)$. Consequently, in the diffusive model, the endemic equilibrium is globally asymptotically stable in $(0, \infty)^{3n}$.

Let us mention additional examples where Theorem 3.1 is applicable. Technical details are similar as in the previous examples, and are left to the reader.

- The paper [18] deals with the global asymptotic stability of the endemic equilibrium for the SIR and SIRS epidemic models (with linear incidence rate). Omitting the differential equation for the susceptible class (instead of the more traditional choice of the removed class), the authors have discovered a new Lyapunov function of the form $V(I,R) = I - I^* \ln I + a(R - R^*)^2$, where $a > 0$. Since this function is a sum of univariate functions with increasing derivatives, Theorem 3.1 is applicable, and yields the global asymptotic stability of the endemic equilibrium for the corresponding system with diffusion.

- A very general form of the SIR model having the form

$$S'(t) = \mu - f(S(t), I(t)) - \mu S(t), \quad I'(t) = f(S(t), I(t)) - \delta I(t),$$

  was considered in [10]. The transmission function f is assumed to be positive in $(0,\infty)^2$, increasing in both variables, concave with respect to the second variable, and such that $f(0, I) = 0 = f(S, 0)$ for all I, $S \in [0, \infty)$. The system always has an infection-free equilibrium $(S_0^*, I_0^*) = (1, 0)$. The basic reproduction number is defined as $R_0 = \frac{1}{\delta}\frac{\partial f}{\partial I}(S_0^*, I_0^*)$. If $R_0 > 1$, the system has a unique positive endemic equilibrium (S_1^*, I_1^*). This equilibrium is globally asymptotically stable in $(0,\infty)^2$; the proof in [10] is based on the Lyapunov function

$$V(S,I) = S - \int_\varepsilon^S \frac{f(S_1^*, I_1^*)}{f(s, I_1^*)}\,\mathrm{d}s + I - \int_\varepsilon^I \frac{f(S_1^*, I_1^*)}{f(S_1^*, i)}\,\mathrm{d}i.$$

  This function is a sum of the univariate functions

$$V_1(S) = S - \int_\varepsilon^S \frac{f(S_1^*, I_1^*)}{f(s, I_1^*)}\,\mathrm{d}s, \quad V_2(I) = I - \int_\varepsilon^I \frac{f(S_1^*, I_1^*)}{f(S_1^*, i)}\,\mathrm{d}i,$$

  whose derivatives

$$V_1'(S) = 1 - \frac{f(S_1^*, I_1^*)}{f(S_1^*, I)}, \quad V_2'(I) = 1 - \frac{f(S_1^*, I_1^*)}{f(S_1^*, I)}$$

  are increasing on $(0, \infty)$. Hence, Theorem 3.1 is applicable, and yields the global asymptotic stability of the endemic equilibrium for the corresponding diffusive system.

- Consider the two-species Lotka-Volterra competition model from Example 2.9. If at least one of the parameters $\alpha, \beta > 0$ is smaller than 1, then the system has a globally asymptotically stable equilibrium where either one of the species becomes extinct, or both species live in coexistence. As shown in [19], the same results hold for the diffusive version (2.12) of this model with $d_1^{ij} = d_1$ and $d_2^{ij} = d_2$ for all $\{i,j\} \in E(G)$; see [19, Theorem 4.5]. The proof is based on Lyapunov functions for the non-diffusive model containing linear terms with positive coefficients and logarithmic terms with negative coefficients (see [19, Lemma 2.1]). Thus, the assumptions of Theorem 3.1 are satisifed, and the global stability results presented in [19, Theorem 4.5] hold even in the more general case with edge-dependent diffusion coefficients.

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