Lotka-Volterra competition model on graphs

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Abstract

We consider a model of two competing species of Lotka-Volterra type with diffusion (migration), where the spatial domain is an arbitrary finite graph (network). Depending on the parameters of the model, we describe the spatially homogeneous stationary states and their stability, discuss the existence and number of spatially heterogeneous stationary states, and study the asymptotic behavior of solutions.

Keywords: competing species, graph, metacommunity, Lotka-Volterra model, diffusion

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1 Introduction

In population dynamics, there exist three basic types of models describing the interaction between two species: predator-prey models, competition models, and mutualism/symbiosis models (Murray, 2002, Chapter 3). This paper focuses on a model of the second type, where two species compete against each other for the same resources. The basic competition model describing this situation is the classical Lotka-Volterra model, which can be written in the form

$$\begin{aligned} u'(t) &= \rho_1 u(t)(1 - u(t) - \alpha v(t)), \\ v'(t) &= \rho_2 v(t)(1 - \beta u(t) - v(t)). \end{aligned} \tag{1.1}$$

The quantities $u(t)$, $v(t)$ correspond to the number of individuals at time t, the parameters ρ_1, ρ_2 are the intrinsic growth rates, and α, β correspond to the strength of the competition; all four parameters are positive. A detailed analysis of this model can be found in a large number of sources devoted to differential equations or mathematical biology, e.g. Murray (2002, Section 3.5).

One drawback of the above-mentioned model is that it does not take into account the spatial distribution of both species. For this reason, various authors have considered the so-called diffusive Lotka-Volterra model, which describes not only the competition between the two species, but also the migration of individuals from each population. The model is expressed as a system of two reaction-diffusion partial differential equations, and was studied in a large number of papers; see e.g. Chen and Hung (2016) and the references cited therein.

On the other hand, mathematical biology often deals with models where the spatial domain consists of discrete patches, corresponding to fragmented habitats (such as islands, ponds, etc.). Such models might be more realistic from the biological viewpoint, and their solutions often display behavior different from that of the continuous-space models. For example, the discrete-space Lotka-Volterra competition model that we consider in the present paper is known to have stable spatially heterogeneous stationary states (Levin, 1974), and this fact is in stark contrast to the continuous-space model, which has no stable nonconstant stationary states (Kishimoto, 1981).

Suppose we have a finite number of discrete patches, each being inhabited by both species. Such a domain can be described by a finite graph $G = (V, E)$, where $V = \{1, \dots, n\}$ is the set of patches, and an edge $\{i, j\} \in E$ means that the species can move between patches i and j. Our model corresponds to the system of differential equations

$$\begin{aligned} u_i'(t) &= d_1 \sum_{j\in N(i)} (u_j(t) - u_i(t)) + \rho_1 u_i(t)(1 - u_i(t) - \alpha v_i(t)), \qquad i \in V, \\ v_i'(t) &= d_2 \sum_{j\in N(i)} (v_j(t) - v_i(t)) + \rho_2 v_i(t)(1 - v_i(t) - \beta u_i(t)), \qquad i \in V, \end{aligned} \tag{1.2}$$

where $d_1, d_2 \geq 0$ are diffusion constants (or migration rates), and $N(i) = \{j \in V; \{i,j\} \in E\}$ denotes the set of all neighbors of a vertex $i \in V$.

In terms of mathematical biology, each species forms a metapopulation – a group of spatially separated populations, where each vertex corresponds to a single habitat. Both species together form a community of metapopulations, which is referred to as a metacommunity. Models involving metapopulations as well as metacommunities have been extensively studied in both biology and mathematics. In particular, numerous authors have considered various problems from population dynamics (predator-prey metapopulations), epidemiology (SIR model) or ecology (survival of endangered species affected by habitat fragmentation). See, for instance, Gilpin and Hanski (1991), Newman (2010) and the references cited therein.

Many sources dealing with metacommunities often either focus on graphs with a small number of vertices (usually two or three), or resort to numerical solution of differential equations in case of larger graphs. Still, the study of dynamical systems on graphs is becoming increasingly popular, and various authors have studied diffusion-type equations on more or less general graphs; see for instance Allen (1987), Chung and Choi (2017), Chung and Park (2017), Cui et al. (2004), Dore and Stosic (2019), Gibert and Yeakel (2019), Hidalgo and Godoy Molina (2010), Newman (2010), Qian (2017), Slavík (2013). Nevertheless, to the best of our knowledge, it seems that a sufficiently detailed analysis of the system (1.2) for general coefficients α, β and a general graph G is still missing, and the goal of this paper is to fill this gap.

The paper is organized as follows: Sections 2 and 3 might be considered as preliminary, while the main results are concentrated in Sections 4 and 5. In Section 2, we begin by recalling some facts about the equilibrium points of the classical Lotka-Volterra competition model and their stability. Moreover, we present some Lyapunov functions (including a new one) that will be needed later. Section 3 is already devoted to the graph model (1.2). We derive a comparison principle, which leads to some a priori bounds and consequently implies global existence and uniqueness of solutions. Section 4 focuses on spatially homogeneous stationary states, in which each species has the same number of individuals at all vertices, and hence there is no diffusion. We determine the stability of these states, and show that if at least one of the parameters α, β is less than 1, then all solutions with positive initial conditions approach one of the homogeneous stationary states. Section 5 is the main part of the paper and focuses primarily on the case where both α and β are greater than 1, i.e., both species are strong competitors. This case is the most interesting one, and the asymptotic behavior of solutions depends on the strength of the diffusion. We show that large diffusion permits only spatially homogeneous stationary states, while small diffusion allows the existence of an exponential number of spatially heteregeneous stationary states in which both species coexist – their tendency to extinction (which is inevitable in a nonspatial model) is compensated by diffusion between the vertices. Finally, Section 6 outlines some possible generalizations and open problems.

Although it is easy to dismiss the model (1.2) as too simple (all patches are identical, with equal carrying capacities and competition coefficients), its dynamical behavior is already quite rich, and the same qualitative properties might be observed in more realistic models that are difficult to analyze. In Section 6, we point out that some results obtained in this paper are still valid for more general models.

Let us highlight some references that are particularly close to the topic of this article: Allen (1983) considers a Lotka-Volterra competition model on general graphs, with a more general diffusion term than (1.2). It is shown that diffusion can lead to extinction of both species, but the result does not apply to (1.2) (as we will see in Theorem 4.2, the extinction state is always unstable for (1.2)). Hastings (1978) considers n-species Lotka-Volterra systems on general graphs, and provides sufficient conditions guaranteeing that all solutions with positive initial values tend to an equilibrium where all species coexist; the result relies on the construction of an appropriate Lyapunov function. We follow a similar approach in Section 4, but consider also the cases where one population is driven to extinction. Along the way, we obtain a result on Lyapunov functions for differential equations on graphs that is not restricted to Lotka-Volterra systems (see Lemma 4.3). Namba (1980) and Redheffer and Zhou (1981) deal with Lotka-Volterra systems on general graphs, but focus on the predator-prey case, and study the problem of global asymptotic stability. Takeuchi (1996) considers n-species Lotka-Volterra systems of the form

$$(u_i^k)'(t) = u_i^k(t)(q_i - f_i(u_1^k(t), \ldots, u_n^k(t))) + \sum_{j \neq k} d_i^{kj}(u_i^j(t) - u_i^k(t)), \quad i \in \{1, \ldots, n\}, \quad k \in V, \tag{1.3}$$

and focuses on the existence of a globally stable positive/nonnegative equilibrium point. Guo and Wu (2011) deal with the bistable case ($\alpha > 1$, $\beta > 1$) of the two-species Lotka-Volterra competition model, but on the infinite lattice $\mathbb{Z}$ instead of a finite graph G, and show the existence of infinitely many stationary states if the diffusion coefficients are small. Our Theorem 5.3 is a counterpart of this result for finite graphs, and the proof relies on different methods. The observation that a two-patch Lotka-Volterra competition model can have stable heterogeneous stationary states goes back to the landmark paper by Levin (1974) (see also the recent survey paper by Gibert and Yeakel (2019)). Here we focus on graphs with n vertices, show that they possess $3^n - 3$ spatially heteregeneous stationary states, and $2^n - 2$ of them are asymptotically stable (in particular, we correct a misleading statement from Levin's paper concerning the total number of equilibria). Finally, we mention the paper by Stehlík (2017), which studies a scalar reaction-diffusion equation on general graphs. It analyzes how the existence/nonexistence of spatially heterogeneous stationary states depends on the strength of the diffusion and reaction, and the results have a close relationship to our Section 5, although the proofs rely on different methods.

2 Some facts about the classical Lotka-Volterra competition model

The goal of this section is to summarize some facts about the classical Lotka-Volterra competition model that will be needed later. This model and the properties of its solutions are described in numerous sources, see e.g. Murray (2002). It consists of two differential equations

$$\begin{aligned} u'(t) &= \rho_1 u(t)(1 - u(t) - \alpha v(t)), \\ v'(t) &= \rho_2 v(t)(1 - \beta u(t) - v(t)), \end{aligned} \tag{2.1}$$

where $\rho_1, \rho_2, \alpha, \beta > 0$ are parameters. To avoid technical difficulties, we restrict ourselves to the case when $\alpha \neq 1$ and $\beta \neq 1$. Also, due to the biological interpretation, we are interested only in nonnegative solutions of (2.1).

The system (2.1) always has at least three equilibria:

$$E_0 = (0, 0), \quad E_1 = (1, 0), \quad E_2 = (0, 1). \tag{2.2}$$

Moreover, if $\alpha\beta \neq 1$, there is a fourth equilibrium

$$E_3 = \left(\frac{1 - \alpha}{1 - \alpha\beta}, \frac{1 - \beta}{1 - \alpha\beta} \right). \tag{2.3}$$

Taking into account our restriction to $\alpha, \beta \neq 1$, we see that E_3 lies in the 1st quadrant if and only if $\alpha > 1$ and $\beta > 1$, or $\alpha < 1$ and $\beta < 1$. In both cases, E_3 is contained in the open square $(0, 1) \times (0, 1)$.

The Jacobian matrix of the system (2.1) is

$$J(u, v) = \begin{pmatrix} \rho_1(1 - 2u - \alpha v) & -\rho_1 \alpha u \\ -\rho_2 \beta v & \rho_2(1 - 2v - \beta u) \end{pmatrix}. \tag{2.4}$$

For $(u, v) = E_0$, the eigenvalues are ρ_1 and ρ_2, and this equilibrium is always unstable. For $(u, v) = E_1$, the eigenvalues are $-\rho_1$ and $\rho_2(1 - \beta)$. This equilibrium is unstable for $\beta < 1$, and asymptotically stable for $\beta > 1$. Similarly, for $(u, v) = E_2$, the eigenvalues are $\rho_1(1 - \alpha)$ and $-\rho_2$. This equilibrium is unstable for $\alpha < 1$, and asymptotically stable for $\alpha > 1$. Finally, for $(u, v) = E_3$, the trace of the Jacobian matrix, which equals the sum of the eigenvalues, is negative. The determinant, which equals the product of the eigenvalues, is $\rho_1\rho_2(\alpha - 1)(\beta - 1)/(1 - \alpha\beta)$. Thus, if $\alpha > 1$ and $\beta > 1$, then the determinant is negative, and E_3 is unstable (a saddle point). If $\alpha < 1$ and $\beta < 1$, then the determinant is positive, and E_3 is asymptotically stable.

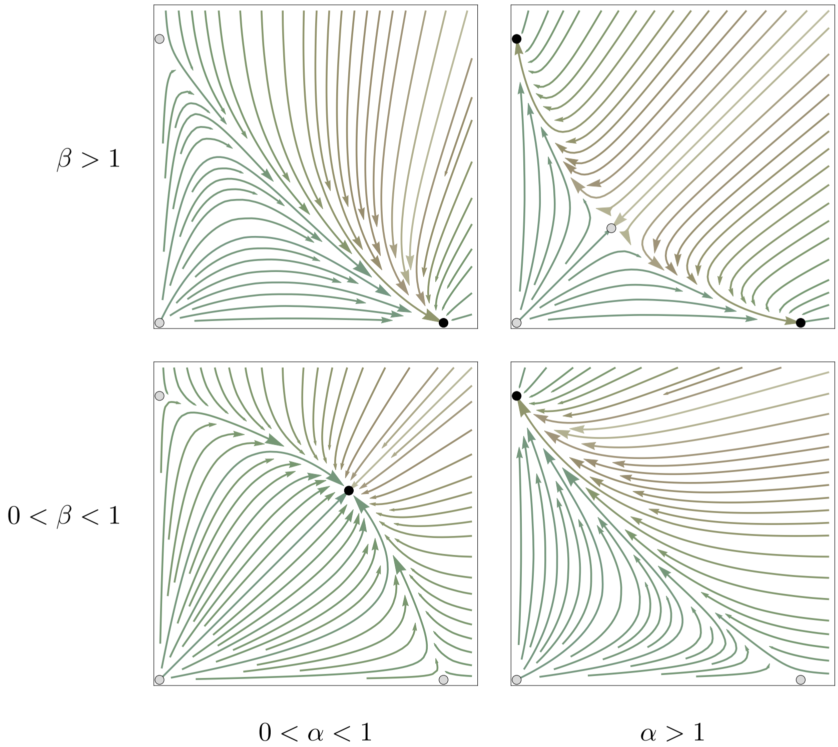

Figure 1: Phase portraits of the classical Lotka-Volterra competition system, depending on the values of α and β. The black/gray points correspond to stable/unstable equilibria.

Except the case $\alpha, \beta > 1$, exactly one of the three equilibrium points E_1, E_2, E_3 is stable. Moreover, it attracts all solutions with positive initial values (see Figure 1). This can be shown by constructing suitable Lyapunov functions; some possible choices are given in the next lemma.

We use the following notation: Given a set $\Omega \subset \mathbb{R}^n$, a differentiable function $V : \Omega \to \mathbb{R}$ and a vector field $f : \Omega \to \mathbb{R}^n$, we denote the orbital derivative of V with respect to f by $\dot{V}$, i.e., we have $\dot{V} = \langle \nabla V, f \rangle$, where $\langle \cdot, \cdot \rangle$ is the standard inner product in $\mathbb{R}^n$. The vector field f will always be clear from the context. It is well known that the orbital derivative is useful for calculating the time derivative of V along solutions of the system $x'(t) = f(x(t))$, since $\frac{\mathrm{d}}{\mathrm{d}t} V(x(t)) = \langle \nabla V(x(t)), x'(t) \rangle = \langle \nabla V(x(t)), f(x(t)) \rangle = \dot{V}(x(t))$.

Lemma 2.1. *Let* $f(u,v) = \begin{pmatrix} \rho_1 u(1-u-\alpha v) \\ \rho_2 v(1-\beta u - v) \end{pmatrix}$*, where* $\rho_1, \rho_2 > 0$.

1. *If* $0 < \alpha < 1$, $0 < \beta < 1$ *and* $(u^*, v^*) = E_3$*, then the function*

$$V(u,v) = \frac{\beta}{\rho_1}(u - u^* - u^* \log(u/u^*)) + \frac{\alpha}{\rho_2}(v - v^* - v^* \log(v/v^*)) \tag{2.5}$$

satisfies $V(u,v) > 0$ *for* $(u,v) \in (0,\infty) \times (0,\infty) \setminus \{E_3\}$, $V(E_3) = 0$, $\dot{V}(u,v) < 0$ *for* $(u,v) \in (0,\infty) \times (0,\infty) \setminus \{E_3\}$*, and* $\dot{V}(E_3) = 0$.

2. *If* $0 < \alpha < 1$ *and* $\beta > 1$*, then the function*

$$V(u,v) = \frac{1}{\rho_1}(u - 1 - \log u) + \frac{1}{\rho_2}(2 - \alpha)v \tag{2.6}$$

satisfies $V(u,v) > 0$ *for* $(u,v) \in (0,\infty) \times [0,\infty) \setminus \{E_1\}$, $V(E_1) = 0$, $\dot{V}(u,v) < 0$ *for* $(u,v) \in (0,\infty) \times [0,\infty) \setminus \{E_1\}$*, and* $\dot{V}(E_1) = 0$.

3. *If $\alpha > 1$ and $0 < \beta < 1$, then the function*

$$V(u,v) = \frac{1}{\rho_1}(2-\beta)u + \frac{1}{\rho_2}(v - 1 - \log v) \tag{2.7}$$

satisfies $V(u,v) > 0$ for $(u,v) \in [0,\infty) \times (0,\infty) \setminus \{E_2\}$, $V(E_2) = 0$, $\dot{V}(u,v) < 0$ for $(u,v) \in [0,\infty) \times [0,\infty) \setminus \{E_2\}$, and $\dot{V}(E_2) = 0$.

Proof. In all three cases, the information about the points where V attains positive or zero values follows easily from the definition of V and the fact that if $x \in (0,\infty)$, then $x - 1 - \log x \geq 0$, and the inequality is strict if $x \neq 1$.

In case 1, we have

$$\begin{aligned}\dot{V}(u,v) &= \frac{\beta}{\rho_1}\left(1 - \frac{u^*}{u}\right)\rho_1 u(1-u-\alpha v) + \frac{\alpha}{\rho_2}\left(1 - \frac{v^*}{v}\right)\rho_2 v(1-\beta u - v)\\ &= \beta(u-u^*)(1-u-\alpha v) + \alpha(v-v^*)(1-\beta u - v)\\ &= \beta(u-u^*)(-(u-u^*) - \alpha(v-v^*)) + \alpha(v-v^*)(-(v-v^*) - \beta(u-u^*)),\end{aligned}$$

where the last equality follows from the fact that $1 - u^* - \alpha v^* = 0$ and $1 - \beta u^* - v^* = 0$. By performing the change of variables $x = u - u^*$ and $y = v - v^*$, we get

$$\dot{V}(x,y) = \beta x(-x - \alpha y) + \alpha y(-y - \beta x) = -\beta x^2 - \alpha y^2 - 2\alpha\beta xy = -\beta(x+\alpha y)^2 + \alpha y^2(\alpha\beta - 1).$$

This expression is always nonpositive, and it vanishes if and only if $(x,y) = (0,0)$. Consequently, $(u,v) \mapsto \dot{V}(u,v)$ is also nonpositive, and it vanishes if and only if $(u,v) = (u^*,v^*) = E_3$.

In case 2, we have

$$\begin{aligned}\dot{V}(u,v) &= \frac{1}{\rho_1}\left(1 - \frac{1}{u}\right)\rho_1 u(1-u-\alpha v) + \frac{1}{\rho_2}(2-\alpha)\rho_2 v(1-\beta u - v)\\ &= (u-1)(1-u-\alpha v) + (2-\alpha)v(1-\beta u - v).\end{aligned}$$

Obviously, $\dot{V}(E_1) = 0$. Our goal is to show that the function

$$h(u,v) = (u-1)(1-u-\alpha v) + (2-\alpha)v(1-\beta u - v), \quad (u,v) \in \mathbb{R}^2$$

satisfies $h < 0$ on $[0,\infty) \times [0,\infty) \setminus \{E_1\}$. First, we check the values on the coordinate axes. For $u = 0$, we have the function $h(0,v) = (\alpha-2)v^2 + 2v - 1$, which has a strict global maximum at $v = \frac{1}{2-\alpha}$; the value of this maximum is $\frac{1-\alpha}{\alpha-2} < 0$, since $\alpha < 1$. For $v = 0$, we get $h(u,0) = -(u-1)^2$, which has a strict global maximum at $u = 1$; the value of this maximum is 0. In summary, h is negative on both axes except at the point E_1, where it vanishes.

The following calculations are best verified using a computer (we used *Wolfram Mathematica*): The gradient of h is the vector

$$\nabla h(u,v) = \begin{pmatrix} -2u + \alpha\beta v - \alpha v - 2\beta v + 2 \\ \alpha\beta u - \alpha u - 2\beta u + 2\alpha v - 4v + 2 \end{pmatrix},$$

which vanishes at the point

$$(u_0,v_0) = \frac{-1}{(\alpha\beta - \alpha - 2\beta)^2 + 4(\alpha-2)}\left(2(\alpha\beta - 3\alpha - 2\beta + 4), 2(\alpha-2)(\beta-1)\right). \tag{2.8}$$

The only exception is when the numerator of the last fraction is zero; for $0 < \alpha < 1$, this happens if and only if $\beta = \frac{\alpha}{\alpha-2} + 2\sqrt{\frac{1}{2-\alpha}}$; this exceptional case will be dealt with later. The quadratic function $(u,v) \mapsto h(u+u_0, v+v_0)$ no longer contains the linear terms:

$$h(u+u_0, v+v_0) = -u^2 + uv(\alpha\beta - \alpha - 2\beta) + (\alpha-2)v^2 - \frac{(\alpha-2)^2(\beta-1)^2}{(\alpha\beta - \alpha - 2\beta)^2 + 4(\alpha-2)}$$

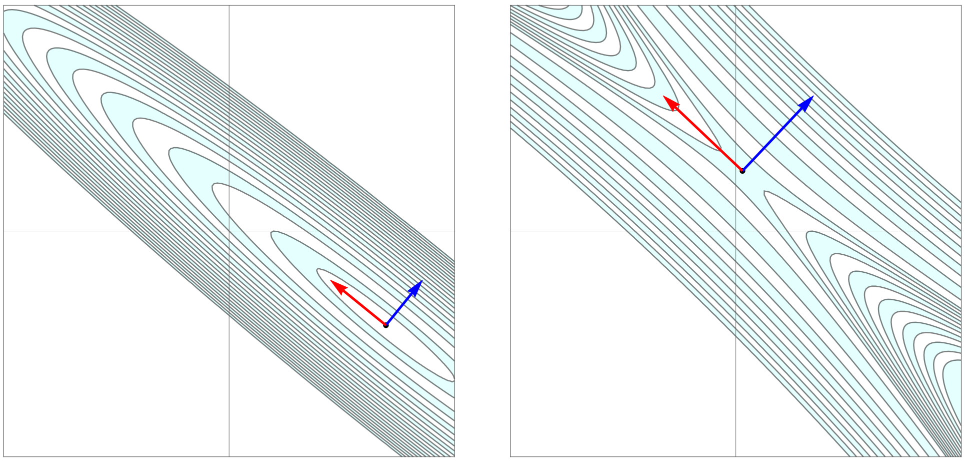

Figure 2: Selected contour lines of the function h. The black point is (u_0, v_0), the red arrow is the eigenvector ϕ_1 and the blue arrow is the eigenvector ϕ_2. On the left is the negative definite case (the picture corresponds to the choices $\alpha = 1/2$, $\beta = 5/4$), the maximum of h in the 1st quadrant is attained on the ellipse tangent to the horizontal axis. On the right is the indefinite case (the picture corresponds to the choices $\alpha = 7/8$, $\beta = 5/4$), the maximum of h in the 1st quadrant is attained on the hyperbola tangent to the horizontal axis.

The first three terms on the right-hand side correspond to a quadratic form, whose discriminant is

$$\Delta = (\alpha\beta - \alpha - 2\beta)^2 + 4(\alpha - 2),$$

i.e., the same expression as in the denominator of (2.8). The matrix of the quadratic form is

$$\begin{pmatrix} -1 & \frac{1}{2}(\alpha\beta - \alpha - 2\beta) \\ \frac{1}{2}(\alpha\beta - \alpha - 2\beta) & \alpha - 2 \end{pmatrix},$$

and it has the following eigenvalues and eigenvectors:

$$\lambda_{1,2} = \frac{1}{2}\left(\pm\sqrt{(\alpha-2)^2\beta^2 - 2(\alpha-2)\alpha\beta + 2(\alpha-1)\alpha + 1} + \alpha - 3\right),$$

$$\phi_{1,2} = \left(\frac{\pm\sqrt{\alpha^2\left(\beta^2 - 2\beta + 2\right) + \alpha\left(-4\beta^2 + 4\beta - 2\right) + 4\beta^2 + 1} + 1 - \alpha}{\alpha(\beta-1) - 2\beta}, 1\right),$$

If $0 < \alpha < 1$ and $1 < \beta < \frac{\alpha}{\alpha-2} + 2\sqrt{\frac{1}{2-\alpha}}$, the discriminant Δ is negative, and the graph of h is an elliptic paraboloid. The contour lines of h are ellipses centered at (u_0, v_0); note that $v_0 < 0$ (see Figure 2, left). Hence, each value of h which is attained in the upper half-plane is also attained somewhere on the u-axis. We already know that the maximum value of h on the u-axis is at $(1, 0)$, and its value is 0. This value cannot be attained elsewhere in the upper half-plane, since then the ellipse corresponding to contour line 0 would intersect the u-axis in two points, which is a contradiction.

If $0 < \alpha < 1$ and $\beta > \frac{\alpha}{\alpha-2} + 2\sqrt{\frac{1}{2-\alpha}}$, the discriminant Δ is positive and the quadratic form is indefinite. The graph of h is a hyperbolic paraboloid, and its contour lines are hyperbolas centered at (u_0, v_0); note that $v_0 > 0$ (see Figure 2, right). The directions of the major axes of these hyperbolas are given by the eigenvectors ϕ_1 and ϕ_2. Since $\lambda_1 > \lambda_2$ and the quadratic form is indefinite, we necessarily have $\lambda_1 > 0$ and $\lambda_2 < 0$. Thus, if we move along the line ℓ_1 passing through (u_0, v_0) in the direction $\pm\phi_1$, the values of h increase with increasing distance from (u_0, v_0); on the other hand, if we move along the perpendicular line ℓ_2 through (u_0, v_0) in the direction $\pm\phi_2$, the values of h decrease with increasing distance from (u_0, v_0). Note also that the components of v_1 have different signs (the first negative and the second positive).

If (u_0, v_0) lies in the first quadrant, then ℓ_1 intersects both positive semiaxes, the maximum of h in the first quadrant is attained on a certain hyperbola with major axis ℓ_1, and therefore the same value also occurs somewhere on the nonnegative semiaxes. But we already know that the maximum value of h on both axes is at $(1, 0)$, and its value is 0. This value cannot be attained elsewhere in the first quadrant, since this would imply the existence of another zero along the nonnegative semiaxes, which is a contradiction.

If (u_0, v_0) lies in the second quadrant, some hyperbolas with major axis ℓ_1 might intersect the first quadrant; the maximum of h then again occurs on the hyperbola which is as far as possible from (u_0, v_0). Otherwise, the maximum will occur on a hyperbola with major axis ℓ_2 which is as close as possible to (u_0, v_0). In both cases, the hyperbola is tangent to one of the nonnegative semiaxes, and the same reasoning as before shows that $h(u, v) < 0$ everywhere in the first quadrant except at the point $(1, 0)$.

Finally, if $0 < \alpha < 1$ and $\beta = \frac{\alpha}{\alpha-2} + 2\sqrt{\frac{1}{2-\alpha}}$, the gradient of h is never zero. Substituting the value of β in the definition of h, we get

$$h(u, v) = -u^2 - 2\sqrt{2-\alpha}uv + 2u + \alpha v^2 - 2v^2 + 2v - 1.$$

The derivative of h in the direction $(1, -1/\sqrt{2-\alpha})$ is

$$\langle \nabla h(u, v), (1, -1/\sqrt{2-\alpha}) \rangle = 2 - \frac{2}{\sqrt{2-\alpha}} > 0,$$

which implies that h is increasing along each line in the direction $(1, -1/\sqrt{2-\alpha})$. Hence, in the upper half-plane, it must have a strict global maximum on the u-axis, which we already know to be at $(1, 0)$.

Case 3 is symmetric to case 2; it suffices to interchange the roles of u and v, α and β. □

Remark 2.2. The Lyapunov function given in part 1 of Lemma 2.1 implies that if $\alpha, \beta < 1$, then E_3 is a globally stable equilibrium for the classical Lotka-Volterra competition model. This fact as well as the Lyapunov function itself are well known (see e.g. Goh, 1976), and we have included the proof of part 1 only for completeness. The Lyapunov functions given in parts 2 and 3 imply the global stability of E_1 or E_2 in the cases $\alpha < 1$ and $\beta > 1$, or $\alpha > 1$ and $\beta < 1$, respectively. The existence of Lyapunov functions of this type was also discussed in the literature but, apparently, only in the less general case when $\alpha\beta < 1$. For example, it is shown in Theorem 3.2.1 of Takeuchi (1996) that a Lotka-Volterra system $x_i' = x_i(b + \sum_{j=1}^{2} a_{ij}x_j)$, $i \in \{1, 2\}$ has a Lyapunov function of the form $V(x_1, x_2) = a(x_1 - 1 - \log x_1) + bx_2$ if the matrix A belongs to a certain class S_w; our system (2.1) corresponds to $A = \begin{pmatrix} -\rho_1 & -\alpha\rho_1 \\ -\beta\rho_2 & -\rho_2 \end{pmatrix}$, and it follows from Exercise 3.2.2 in Takeuchi (1996) that $A \in S_w$ if and only if $\alpha\beta < 1$.

For our purposes, it is important that all Lyapunov functions from Lemma 2.1 have the form $a + bu + c\log u + dv + e\log v$; this will make it possible to apply Lemma 4.3 and get Lyapunov functions for the Lotka-Volterra system on graphs. Other Lyapunov functions available in the literature, such as the quadratic functions described by Tang et al. (2013), cannot be used for the same purpose.

3 Basic results for the competition model on graphs

We now turn our attention to the competition model described in the introduction of the paper, i.e., we consider the system

$$\begin{aligned} u_i'(t) &= d_1 \sum_{j\in N(i)} (u_j(t) - u_i(t)) + \rho_1 u_i(t)(1 - u_i(t) - \alpha v_i(t)), \qquad i \in V, \\ v_i'(t) &= d_2 \sum_{j\in N(i)} (v_j(t) - v_i(t)) + \rho_2 v_i(t)(1 - v_i(t) - \beta u_i(t)), \qquad i \in V, \end{aligned} \tag{3.1}$$

where $V = \{1, \ldots, n\}$ is the vertex set of a graph G.

For special choices of the graph G, the system (3.1) corresponds to the space-discretized version of the reaction-diffusion system

$$\begin{aligned} \partial_t u(x, t) &= d_1 \nabla^2 u(x, t) + \rho_1 u(x, t)(1 - u(x, t) - \alpha v(x, t)), \\ \partial_t v(x, t) &= d_2 \nabla^2 v(x, t) + \rho_2 v(x, t)(1 - v(x, t) - \beta u(x, t)) \end{aligned} \tag{3.2}$$

on a bounded n-dimensional spatial domain with Neumann boundary conditions. Depending on the dimension n, spatial discretization of (3.2) leads to the system (3.1) with G being a path graph when $n = 1$, or a (subset of) grid/lattice graph when $n > 1$.

As we will see, the system (3.1) shares some properties with (3.2), such as the validity of the maximum principle (see Corollary 3.4), or the asymptotic behavior of solutions when at least one of the parameters α, β is less than 1 (see Theorem 4.5). Nevertheless, there are also significant differences between (3.1) and (3.2); in contrast to (3.2), the discrete-space system (3.1) can have a large number of stable spatially heterogeneous stationary states (see Theorem 5.6) if $\alpha > 1$ and $\beta > 1$. Moreover, as mentioned in the introduction, the system (3.2) is a mathematical model of competition between two species in a patchy environment, where it is more natural than (3.2), and makes sense for an arbitrary graph G.

The goal of this section is to collect some basic results for the system (3.1), such as the global existence of solutions, and a comparison principle. The results are simple, make no claim for originality, and might be derived by other methods. Nevertheless, they will be needed throughout the rest of the paper, and are included for completeness.

The system (3.1) might be rewritten in the vector form

$$\begin{aligned} u'(t) &= -d_1 Lu(t) + \rho_1 f_1(u(t), v(t)), \\ v'(t) &= -d_2 Lv(t) + \rho_2 f_2(u(t), v(t)), \end{aligned} \tag{3.3}$$

where $f_1, f_2 : \mathbb{R}^{2n} \to \mathbb{R}^n$ are given by

$$f_1(u, v) = \begin{pmatrix} u_1(1 - u_1 - \alpha v_1) \\ \cdots \\ u_n(1 - u_n - \alpha v_n) \end{pmatrix}, \quad f_2(u, v) = \begin{pmatrix} v_1(1 - v_1 - \beta u_1) \\ \cdots \\ v_n(1 - v_n - \beta u_n) \end{pmatrix}, \tag{3.4}$$

and $L = \{l_{ij}\}_{i,j=1}^n$ is the Laplacian matrix of G given by

$$l_{ij} = \begin{cases} \deg(i) & \text{if } i = j, \\ -1 & \text{if } i \neq j \text{ and } \{i, j\} \in E, \\ 0 & \text{otherwise.} \end{cases} \tag{3.5}$$

From now on, we always assume that G is a connected graph (otherwise, it is possible to treat each component separately). In this case, it is well known that L has a simple zero eigenvalue with the corresponding eigenspace being spanned by the vector $(1, \dots, 1)$, and all remaining eigenvalues are positive (see e.g. Chapter 4 in Bapat (2010)).

Our first goal is to obtain a comparison theorem for (3.1). If $x, y \in \mathbb{R}^n$, then the notation $x \leq y$ means $x_i \leq y_i$ for all $i \in \{1, \dots, n\}$. It might be expected that if u^1, v^1 and u^2, v^2 are two solutions of (3.1) satisfying $0 \leq u^1(0) \leq u^2(0)$ and $0 \leq v^1(0) \leq v^2(0)$, then $u^1(t) \leq u^2(t)$ and $v^1(t) \leq v^2(t)$ for all t. However, such an assertion is, in general, false, as demonstrated by the following example.

Example 3.1. Consider solutions with the initial conditions $u_i^1(0) = v_i^1(0) = u_i^2(0) = 1/2$ and $v_i^2(0) = 1$ for all $i \in V$. Then (3.1) implies

$$(u_i^1)'(0) = \frac{\rho_1}{2}\left(\frac{1}{2} - \frac{\alpha}{2}\right), \quad (u_i^2)'(0) = \frac{\rho_1}{2}\left(\frac{1}{2} - \alpha\right) \quad \text{for all } i \in V, \tag{3.6}$$

i.e., $(u_i^2)'(0) < (u_i^1)'(0)$, wherefrom it follows that $u_i^2(t) < u_i^1(t)$ on a right open neighborhood of 0.

However, we can show that solutions of the system (3.1) with nonnegative initial conditions can be majorized by solutions of a decoupled system which has no interaction between the two species. (A similar comparison theorem for systems of partial differential equations can be found in Valero (2012, Theorem 4.1), but our derivation is different.)

Theorem 3.2. *Let $I \subset \mathbb{R}$ be an interval with $\min I = 0$. Suppose that $u^1, v^1 : I \to \mathbb{R}^n$ satisfy*

$$\begin{aligned} (u_i^1)'(t) &= d_1 \sum_{j \in N(i)} (u_j^1(t) - u_i^1(t)) + \rho_1 u_i^1(t)(1 - u_i^1(t) - \alpha v_i^1(t)), \qquad i \in V, \\ (v_i^1)'(t) &= d_2 \sum_{j \in N(i)} (v_j^1(t) - v_i^1(t)) + \rho_2 v_i^1(t)(1 - v_i^1(t) - \beta u_i^1(t)), \qquad i \in V, \end{aligned} \tag{3.7}$$

and $u^2, v^2 : I \to \mathbb{R}^n$ satisfy

$$
\begin{aligned}
(u_i^2)'(t) &= d_1 \sum_{j\in N(i)} (u_j^2(t) - u_i^2(t)) + \rho_1 u_i^2(t)(1 - u_i^2(t)), \qquad i \in V,\\
(v_i^2)'(t) &= d_2 \sum_{j\in N(i)} (v_j^2(t) - v_i^2(t)) + \rho_2 v_i^2(t)(1 - v_i^2(t)), \qquad i \in V.
\end{aligned}
\tag{3.8}
$$

If $0 \le u^1(0) \le u^2(0)$ and $0 \le v^1(0) \le v^2(0)$, then $u^1(t) \le u^2(t)$ and $v^1(t) \le v^2(t)$ for all $t \in I$.

Proof. To prove the theorem, it suffices to consider (3.7) and (3.8) as a $4n$-dimensional system

$$
\frac{\mathrm{d}}{\mathrm{d}t}(u^1(t), v^1(t), u^2(t), v^2(t)) = f(u^1(t), v^1(t), u^2(t), v^2(t)), \tag{3.9}
$$

(where f is constructed from the reaction functions in (3.7) and (3.8)) and show that the set

$$
S = \{(u^1, v^1, u^2, v^2) \in \mathbb{R}^n \times \mathbb{R}^n \times \mathbb{R}^n \times \mathbb{R}^n; u^1 \ge 0, v^1 \ge 0, u^1 \le u^2, v^1 \le v^2\}
$$

is a positively invariant region. To achieve this goal, we use Bony's theorem (see e.g. Clarke (1975, Corollary 4.10)). The right-hand side f of (3.9) is continuously differentiable, and therefore locally Lipschitz-continuous. The set S is closed, convex, and can be written in the form

$$
S = \bigcap_{i=1}^n S_i^1 \cap \bigcap_{i=1}^n S_i^2 \cap \bigcap_{i=1}^n S_i^3 \cap \bigcap_{i=1}^n S_i^4,
$$

where $S_i^k = \{(u^1, v^1, u^2, v^2) \in \mathbb{R}^n \times \mathbb{R}^n \times \mathbb{R}^n \times \mathbb{R}^n; G_i^k(u^1, v^1, u^2, v^2) \le 0\}$, and

$$
\begin{aligned}
G_i^1(u^1, v^1, u^2, v^2) &= -u_i^1, & i &\in \{1, \dots, n\},\\
G_i^2(u^1, v^1, u^2, v^2) &= -v_i^1, & i &\in \{1, \dots, n\},\\
G_i^3(u^1, v^1, u^2, v^2) &= u_i^1 - u_i^2, & i &\in \{1, \dots, n\},\\
G_i^4(u^1, v^1, u^2, v^2) &= v_i^1 - v_i^2, & i &\in \{1, \dots, n\}
\end{aligned}
$$

are continuously differentiable functions.

Bony's theorem requires us to verify that if $x \in \partial S$ and ν is an outward normal to S at x, then $\langle \nu, f(x)\rangle \le 0$. Since S is convex, outward normals in Bony's sense coincide with outward normals in the sense of convex analysis (i.e., they are normals to supporting hyperplanes pointing to the half-space that does not contain S). If $x \in \partial S$, then $x \in \partial S_i^k \cap S$ for a certain $k \in \{1, 2, 3, 4\}$ and $i \in \{1, \dots, n\}$. If there is only one such pair (k, i), then all outward unit normals ν to the boundary of S at x are positive multiples of $\nabla G_i^k(x)$. On the other hand, if x is a boundary point of several sets S_i^k, then each outward normal ν to the boundary of S at x is a linear combination of the corresponding vectors $\nabla G_i^k(x)$ with nonnegative coefficients (see Schneider (2014, Theorem 2.2.1)). Hence, to verify that $\langle \nu, f(x)\rangle \le 0$, it suffices to show that $\langle \nabla G_i^k(x), f(x)\rangle \le 0$ for all $x \in \partial S_i^k \cap S$.

If $(u^1, v^1, u^2, v^2) \in \partial S_i^1 \cap S$, then $u_j^1 \ge 0$ for $j \in \{1, \dots, n\}$, $u_i^1 = 0$, and $\nabla G_i^1(u^1, v^1, u^2, v^2)$ is the vector whose i-th component is -1 and the remaining ones are zero. Therefore,

$$
\langle \nabla G_i^1(u^1, v^1, u^2, v^2), f(u^1, v^1, u^2, v^2)\rangle = -\left(d_1 \sum_{j\in N(i)} (u_j^1 - u_i^1) + \rho_1 u_i^1(1 - u_i^1 - \alpha v_i^1)\right) \le 0.
$$

Similarly, if $(u^1, v^1, u^2, v^2) \in \partial S_i^2 \cap S$, then $v_j^1 \ge 0$ for $j \in \{1, \dots, n\}$, $v_i^1 = 0$, and $\nabla G_i^2(u^1, v^1, u^2, v^2)$ is the vector whose $(n+i)$-th component is -1 and the remaining ones are zero. Therefore,

$$
\langle \nabla G_i^2(u^1, v^1, u^2, v^2), f(u^1, v^1, u^2, v^2)\rangle = -\left(d_2 \sum_{j\in N(i)} (v_j^1 - v_i^1) + \rho_2 v_i^1(1 - v_i^1 - \beta u_i^1)\right) \le 0.
$$

If $(u^1, v^1, u^2, v^2) \in \partial S_i^3 \cap S$, then $u_j^1 \le u_j^2$ for all $j \in \{1, \dots, n\}$, $0 \le u_i^1 = u_i^2$, $0 \le v_i^1$, and $\nabla G_i^3(u^1, v^1, u^2, v^2)$ is the vector whose i-th component is 1, $(2n+i)$-th component is -1, and the remaining ones are zero. Therefore,

$$\langle \nabla G_i^3(u^1, v^1, u^2, v^2), f(u^1, v^1, u^2, v^2)\rangle = d_1 \sum_{j \in N(i)} (u_j^1 - u_i^1) + \rho_1 u_i^1 (1 - u_i^1 - \alpha v_i^1)$$

$$- \left(d_1 \sum_{j \in N(i)} (u_j^2 - u_i^2) + \rho_1 u_i^2 (1 - u_i^2) \right) \le \rho_1 [u_i^1 (1 - u_i^1 - \alpha v_i^1) - u_i^2 (1 - u_i^2)] = -\rho_1 u_i^1 \alpha v_i^1 \le 0.$$

Similarly, if $(u^1, v^1, u^2, v^2) \in \partial S_i^4 \cap S$, then $v_j^1 \le v_j^2$ for all $j \in \{1, \dots, n\}$, $0 \le v_i^1 = v_i^2$, $0 \le u_i^1$, and $\nabla G_i^4(u^1, v^1, u^2, v^2)$ is the vector whose $(n+i)$-th component is 1, $(3n+i)$-th component is -1, and the remaining ones are zero. Therefore,

$$\langle \nabla G_i^4(u^1, v^1, u^2, v^2), f(u^1, v^1, u^2, v^2)\rangle = d_2 \sum_{j \in N(i)} (v_j^1 - v_i^1) + \rho_2 v_i^1 (1 - v_i^1 - \beta u_i^1)$$

$$- \left(d_2 \sum_{j \in N(i)} (v_j^2 - v_i^2) + \rho_2 v_i^2 (1 - v_i^2) \right) \le \rho_2 [v_i^1 (1 - v_i^1 - \beta u_i^1) - v_i^2 (1 - v_i^2)] = -\rho_2 v_i^1 \beta u_i^1 \le 0.$$

Hence, the assumptions of Bony's theorem are satisfied, and S is a positively invariant region for the $4n$-dimensional system (3.9), which completes the proof. □

Another basic fact about the system (3.1) is that solutions with nonnegative initial conditions remain nonnegative for all time.

Theorem 3.3. *Let $I \subset \mathbb{R}$ be an interval with $\min I = 0$. If $u, v : I \to \mathbb{R}^n$ satisfy (3.1) and $u(0), v(0) \ge 0$, then $u(t) \ge 0$ and $v(t) \ge 0$ for all $t \in I$.*

Proof. The statement is equivalent to the fact that the set

$$S = \{(u^1, v^1) \in \mathbb{R}^n \times \mathbb{R}^n; u^1 \ge 0, v^1 \ge 0\}$$

is a positively invariant region for the system (3.1). This can be shown using Bony's theorem; since the calculations are essentially identical to those performed in the proof of Theorem 3.2, we omit the details. □

As an easy corollary of Theorems 3.2 and 3.3, we get the following a priori bounds for solutions of the system (3.1).

Corollary 3.4. *Let $I \subset \mathbb{R}$ be an interval with $\min I = 0$. Suppose that $u, v : I \to \mathbb{R}^n$ satisfy (3.1) and $u(0), v(0) \ge 0$. If $\tilde{u} = \max\{u_1(0), u_2(0), \dots, u_n(0)\}$ and $\tilde{v} = \max\{v_1(0), v_2(0), \dots, v_n(0)\}$, then*

$$\begin{aligned} 0 \le u(t) &\le \frac{\tilde{u}}{\tilde{u} + e^{-t\rho_1}(1 - \tilde{u})} \le \max\{1, \tilde{u}\}, \\ 0 \le v(t) &\le \frac{\tilde{v}}{\tilde{v} + e^{-t\rho_1}(1 - \tilde{v})} \le \max\{1, \tilde{v}\} \end{aligned} \tag{3.10}$$

for all $t \in I$.

Proof. According to Theorems 3.2 and 3.3, the solution u, v is nonnegative and majorized by the solution u^2, v^2 of the system (3.8) with initial conditions $u_i^2(0) = \tilde{u}$ and $v_i^2(0) = \tilde{v}$ for all $i \in V$. Since $u_1^2(t) = \cdots = u_n^2(t)$ and $v_1^2(t) = \cdots = v_n^2(t)$ for $t = 0$, it is easy to check that these equalities hold for all $t \in I$, and u_i^2 and v_i^2 satisfy the logistic equations

$$\begin{aligned} (u_i^2)'(t) &= \rho_1 u_i^2(t)(1 - u_i^2(t)), \qquad u_i^2(0) = \tilde{u}, \\ (v_i^2)'(t) &= \rho_2 v_i^2(t)(1 - v_i^2(t)), \qquad v_i^2(0) = \tilde{v}. \end{aligned}$$

The proof is finished by observing that the solution of the logistic equation $x'(t) = \rho x(t)(1 - x(t))$ with $x(0) \geq 0$ is given by the formula

$$x(t) = \frac{x(0)}{x(0) + e^{-t\rho}(1 - x(0))},$$

and satisfies $x(t) \leq \max\{1, x(0)\}$ for all $t \geq 0$. $\square$

According to Corollary 3.4, solutions of the system (3.1) with nonnegative initial conditions remain in a compact subset of $\mathbb{R}^{2n}$ for all time, and therefore cannot blow up. Since the right-hand side of (3.1) is continuously differentiable and therefore locally Lipschitz-continuous, we obtain global existence and uniqueness of solutions to the system (3.1) with nonnegative initial conditions.

4 Homogeneous stationary states and global stability

Let us look for stationary states of the system (3.1) having the form $u_i(t) = u^* \geq 0$ and $v_i(t) = v^* \geq 0$ for all $i \in V$, $t \geq 0$; such equilibria will be called spatially *homogeneous* (as opposed to spatially *heterogeneous* equilibria, where the components of u or v need not coincide). Substituting into (3.1), we get

$$\begin{aligned} 0 &= \rho_1 u^*(1 - u^* - \alpha v^*), \\ 0 &= \rho_2 v^*(1 - v^* - \beta u^*). \end{aligned} \tag{4.1}$$

Hence, a pair $E = (u^*, v^*)$ determines a homogeneous stationary state of the system (3.1) if and only if E is a stationary state of the classical Lotka-Volterra system (2.1), i.e., if E coincides with one of the four equilibrium points E_0, E_1, E_2, E_3 introduced in Section 2.

We will use the symbol $\boldsymbol{E}_i$ to denote the homogeneous stationary state of the system (3.1) satisfying $(u_i(t), v_i(t)) = E_i$ for all $i \in V$, $t \geq 0$. Note that we use boldface to distinguish homogeneous stationary states of (3.1) from stationary states of (2.1). Thus, $\boldsymbol{E}_i \in \mathbb{R}^{2n}$, while $E_i \in \mathbb{R}^2$.

Let us determine the stability of the homogeneous stationary states.

Lemma 4.1. *If E_i is an unstable stationary state of the system* (2.1)*, then $\boldsymbol{E}_i$ is an unstable homogeneous stationary state of the system* (3.1)*.*

Proof. If $t \mapsto (u(t), v(t))$ is an arbitrary solution of the two-dimensional system (2.1), then the functions given by $u_j(t) = u(t)$ and $v_j(t) = v(t)$ for all $j \in V$, $t \geq 0$, provide a solution of the system (3.1). Thus, if there exists a neighborhood of E_i such that solutions of (2.1) starting arbitrarily close to E_i leave this neighborhood, then there also exists a neighborhood of $\boldsymbol{E}_i$ such that solutions of (3.1) starting arbitrarily close to $\boldsymbol{E}_i$ leave this neighborhood. $\square$

Theorem 4.2. *Suppose that $\alpha, \beta > 0$ and $\alpha, \beta \neq 1$. Then the following statements hold:*

- $\boldsymbol{E}_0$ *is always unstable.*
- $\boldsymbol{E}_1$ *is unstable if $\beta < 1$, and asymptotically stable if $\beta > 1$.*
- $\boldsymbol{E}_2$ *is unstable if $\alpha < 1$, and asymptotically stable if $\alpha > 1$.*
- $\boldsymbol{E}_3$ *is unstable if $\alpha > 1$ and $\beta > 1$, and asymptotically stable if $\alpha < 1$ and $\beta < 1$.*

Proof. As a consequence of Lemma 4.1, the conditions for the instability of $\boldsymbol{E}_i$ as a stationary state of (3.1) follow from the conditions for the instability of E_i as a stationary state of the classical Lotka-Volterra system (2.1). It remains to prove the assertions concerning asymptotic stability. According to (3.3), the system (3.1) can be written in the form

$$\begin{pmatrix} u' \\ v' \end{pmatrix} = \begin{pmatrix} -d_1 L & 0 \\ 0 & -d_2 L \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix} + \begin{pmatrix} \rho_1 f_1(u,v) \\ \rho_2 f_2(u,v) \end{pmatrix},$$

where L is the Laplacian matrix of G, and $f_1, f_2 : \mathbb{R}^{2n} \to \mathbb{R}^n$ are defined in (3.4). The Jacobian matrix of the right-hand side is

$$\begin{pmatrix} -d_1 L & 0 \\ 0 & -d_2 L \end{pmatrix} + \begin{pmatrix} \rho_1 \frac{\partial f_{1,1}}{\partial u_1} & & & \rho_1 \frac{\partial f_{1,1}}{\partial v_1} & & \\ & \ddots & & & \ddots & \\ & & \rho_1 \frac{\partial f_{1,n}}{\partial u_n} & & & \rho_1 \frac{\partial f_{1,n}}{\partial v_n} \\ \rho_2 \frac{\partial f_{2,1}}{\partial u_1} & & & \rho_2 \frac{\partial f_{2,1}}{\partial v_1} & & \\ & \ddots & & & \ddots & \\ & & \rho_2 \frac{\partial f_{2,n}}{\partial u_n} & & & \rho_2 \frac{\partial f_{2,n}}{\partial v_n} \end{pmatrix},$$

where $f_{k,i}$ denotes the i-th component of f_k. By permuting the rows and columns, we obtain the matrix

$$\begin{pmatrix} -d_1 l_{11} & 0 & \cdots & -d_1 l_{1n} & 0 \\ 0 & -d_2 l_{11} & \cdots & 0 & -d_2 l_{1n} \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ -d_1 l_{n1} & 0 & \cdots & -d_1 l_{nn} & 0 \\ 0 & -d_2 l_{n1} & \cdots & 0 & -d_2 l_{nn} \end{pmatrix} + \begin{pmatrix} \rho_1 \frac{\partial f_{1,1}}{\partial u_1} & \rho_1 \frac{\partial f_{1,1}}{\partial v_1} & & & \\ \rho_2 \frac{\partial f_{2,1}}{\partial u_1} & \rho_2 \frac{\partial f_{2,1}}{\partial v_1} & & & \\ & & \ddots & & \\ & & & \rho_1 \frac{\partial f_{1,n}}{\partial u_n} & \rho_1 \frac{\partial f_{1,n}}{\partial v_n} \\ & & & \rho_2 \frac{\partial f_{2,n}}{\partial u_n} & \rho_2 \frac{\partial f_{2,n}}{\partial v_n} \end{pmatrix}. \tag{4.2}$$

Since the rows and columns were permuted in the same way, the eigenvalues are preserved. If we substitute $(u_j, v_j) = E_i$ for each $j \in V$, then the matrix (4.2) becomes simply

$$L \otimes \begin{pmatrix} -d_1 & 0 \\ 0 & -d_2 \end{pmatrix} + I_n \otimes J(E_i), \tag{4.3}$$

where $\otimes$ is the Kronecker product of matrices, I_n is the identity matrix of order n, and $J(E_i)$ is the 2×2 Jacobian matrix of the classical Lotka-Volterra system, i.e., the matrix $J(u, v)$ from (2.4) with $(u, v) = E_i$. Since the matrices L and I_n are simultaneously diagonalizable, a result by Friedman (1961, Theorem 1) implies that the eigenvalues of (4.3) coincide with the eigenvalues of the matrices

$$J(E_i) + \lambda \begin{pmatrix} -d_1 & 0 \\ 0 & -d_2 \end{pmatrix}, \tag{4.4}$$

where λ is an eigenvalue of L. (Note that the definition of the Kronecker product in Friedman (1961) differs from the standard one: our $A \otimes B$ corresponds to $B \otimes A$ as defined in Friedman (1961, p. 39).) For $i = 1$, (4.4) becomes the matrix

$$\begin{pmatrix} -\rho_1 - \lambda d_1 & -\rho_1 \alpha \\ 0 & \rho_2(1-\beta) - \lambda d_2 \end{pmatrix}.$$

Its eigenvalues are the diagonal elements, which are negative if $\beta > 1$ (recall that all the eigenvalues λ are nonnegative).

For $i = 2$, (4.4) becomes the matrix

$$\begin{pmatrix} \rho_1(1-\alpha) - \lambda d_1 & 0 \\ -\rho_2 \beta & -\rho_2 - \lambda d_2 \end{pmatrix},$$

whose eigenvalues are negative if $\alpha > 1$.

Finally, for $i = 3$, (4.4) becomes the matrix

$$\begin{pmatrix} \frac{\rho_1(\alpha-1)}{1-\alpha\beta} - \lambda d_1 & \frac{\rho_1 \alpha(\alpha-1)}{1-\alpha\beta} \\ \frac{\rho_2 \beta(\beta-1)}{1-\alpha\beta} & \frac{\rho_2(\beta-1)}{1-\alpha\beta} - \lambda d_2 \end{pmatrix}.$$

If $\alpha < 1$ and $\beta < 1$, the trace is negative, and the determinant equals

$$\frac{\rho_1 \rho_2 (\alpha-1)(\beta-1)}{1-\alpha\beta} - \lambda d_1 \frac{\rho_2(\beta-1)}{1-\alpha\beta} - \lambda d_2 \frac{\rho_1(\alpha-1)}{1-\alpha\beta} + \lambda^2 d_1 d_2,$$

which is positive since the first summand is positive and the remaining three nonnegative. Hence, both eigenvalues of the above-mentioned matrix have to be negative. $\square$

The next lemma provides a method for constructing Lyapunov functions for diffusion-type equations on graphs.

Lemma 4.3. *Let $M \subset \mathbb{R}^2$ and consider a function $V : M \to \mathbb{R}$ having the form*

$$V(u,v) = a + bu + c\log u + dv + e\log v \tag{4.5}$$

with $c, e \leq 0$. Given a vector field $h : \mathbb{R}^2 \to \mathbb{R}^2$, suppose that $\dot{V}(u,v) \leq 0$ for all $(u,v) \in M$. Then the orbital derivative of the function

$$W(u_1,\dots,u_n,v_1,\dots,v_n) = \sum_{i=1}^{n} V(u_i,v_i) \tag{4.6}$$

with respect to the vector field

$$F(u_1,\dots,u_n,v_1,\dots,v_n) = \begin{pmatrix} d_1\sum_{j\in N(1)}(u_j-u_1)+h_1(u_1,v_1) \\ \cdots \\ d_1\sum_{j\in N(n)}(u_j-u_n)+h_1(u_n,v_n) \\ d_2\sum_{j\in N(1)}(v_j-v_1)+h_2(u_1,v_1) \\ \cdots \\ d_2\sum_{j\in N(n)}(v_j-v_n)+h_2(u_n,v_n) \end{pmatrix} \tag{4.7}$$

satisfies

$$\dot{W}(u_1,\dots,u_n,v_1,\dots,v_n) \leq 0 \tag{4.8}$$

whenever $(u_i,v_i) \in M$ for all $i \in \{1,\dots,n\}$. Moreover, the equality $\dot{W}(u_1,\dots,u_n,v_1,\dots,v_n) = 0$ holds if and only if the following conditions are satisfied:

- $\sum_{i=1}^{n} \dot{V}(u_i,v_i) = 0$.
- *If $c, d_1 \neq 0$, then $u_1 = \cdots = u_n$*
- *If $e, d_2 \neq 0$, then $v_1 = \cdots = v_n$.*

Proof. We calculate

$$\begin{aligned}
\dot{W}(u,v) &= \sum_{i=1}^{n} \frac{\partial W}{\partial u_i}(u,v)\left(d_1\sum_{j\in N(i)}(u_j-u_i)+h_1(u_i,v_i)\right) + \sum_{i=1}^{n} \frac{\partial W}{\partial v_i}(u,v)\left(d_2\sum_{j\in N(i)}(v_j-v_i)+h_2(u_i,v_i)\right) \\
&= \sum_{i=1}^{n} \frac{\partial V}{\partial u}(u_i,v_i)\left(d_1\sum_{j\in N(i)}(u_j-u_i)+h_1(u_i,v_i)\right) + \sum_{i=1}^{n} \frac{\partial V}{\partial v}(u_i,v_i)\left(d_2\sum_{j\in N(i)}(v_j-v_i)+h_2(u_i,v_i)\right) \\
&= d_1\sum_{i=1}^{n} \frac{\partial V}{\partial u}(u_i,v_i)\sum_{j\in N(i)}(u_j-u_i) + d_2\sum_{i=1}^{n} \frac{\partial V}{\partial v}(u_i,v_i)\sum_{j\in N(i)}(v_j-v_i) + \sum_{i=1}^{n}\dot{V}(u_i,v_i) \\
&\leq d_1\sum_{i=1}^{n}\left(b+\frac{c}{u_i}\right)\sum_{j\in N(i)}(u_j-u_i) + d_2\sum_{i=1}^{n}\left(d+\frac{e}{v_i}\right)\sum_{j\in N(i)}(v_j-v_i) \\
&= d_1 b\sum_{i=1}^{n}\sum_{j\in N(i)}(u_j-u_i) + d_2 d\sum_{i=1}^{n}\sum_{j\in N(i)}(v_j-v_i) + d_1 c\sum_{i=1}^{n}\sum_{j\in N(i)}\left(\frac{u_j}{u_i}-1\right) + d_2 e\sum_{i=1}^{n}\sum_{j\in N(i)}\left(\frac{v_j}{v_i}-1\right).
\end{aligned}$$

The first double sum on the right-hand side is zero: For an arbitrary edge $\{x,y\} \in E$, the double sum contains the term $u_x - u_y$, as well as $u_y - u_x$. For the same reason, the second double sum is also zero. Because $c, e \leq 0$ and $d_1, d_2 \geq 0$, it suffices to show that the third and fourth double sums are nonnegative. To see this, note that

$$\sum_{i=1}^{n}\sum_{j\in N(i)}\left(\frac{u_j}{u_i}-1\right) = \sum_{i=1}^{n}\sum_{j\in N(i)}\frac{u_j}{u_i} - 2|E| = \sum_{\{i,j\}\in E}\left(\frac{u_j}{u_i}+\frac{u_i}{u_j}\right) - 2|E|.$$

Since $z + 1/z \geq 2$ for all $z \in (0, \infty)$, we see that the right-hand side of the last equality is nonnegative. This proves the first part of the lemma.

An inspection of the proof easily yields the necessary and sufficient conditions for equality to occur in the proved inequality. In particular, note that $\sum_{\{i,j\}\in E}\left(\frac{u_j}{u_i} + \frac{u_i}{u_j}\right) - 2|E| = 0$ if and only $\frac{u_j}{u_i} + \frac{u_i}{u_j} = 2$ whenever $\{i, j\} \in E$. This is equivalent to $u_i = u_j$ whenever $\{i, j\} \in E$. Since the graph is connected, we conclude that $u_1 = \cdots = u_n$; similar considerations apply to $v_1, \ldots, v_n$. □

Remark 4.4. The observation that if V is the Lyapunov function given in part 1 of Lemma 2.1, then $\sum_{i=1}^{n} V(u_i, v_i)$ is a Lyapunov function for the system (3.1), goes back to Hastings (1978, Theorem 3), but no proof is given there. Our result from Lemma 4.3 is not restricted to Lotka-Volterra systems, and applies to a wider class of Lyapunov functions. A very general result on the construction of Lyapunov functions for differential equations on graphs is given in Li and Shuai (2010), but it is unclear whether it is applicable to our problem. (Pages 6–7 of Li and Shuai (2010) deal with a Lotka-Volterra model, but consider only the Lyapunov function having the form given in part 1 of Lemma 2.1.)

The next result describes the asymptotic behavior of solutions to (3.1) in all cases when at least one of the parameters α, β is less than 1.

Theorem 4.5. *If $d_1, d_2, \rho_1, \rho_2 > 0$, then the following statements hold:*

- *If $0 < \alpha < 1$ and $\beta > 1$, then an arbitrary solution $u, v : [0, \infty) \to \mathbb{R}^n$ of (3.1) with $u(0) > 0$ and $v(0) \geq 0$ approaches $\boldsymbol{E}_1$ as $t \to \infty$.*
- *If $\alpha > 1$ and $0 < \beta < 1$, then an arbitrary solution $u, v : [0, \infty) \to \mathbb{R}^n$ of (3.1) with $u(0) \geq 0$ and $v(0) > 0$ approaches $\boldsymbol{E}_2$ as $t \to \infty$.*
- *If $0 < \alpha < 1$ and $0 < \beta < 1$, then an arbitrary solution $u, v : [0, \infty) \to \mathbb{R}^n$ of (3.1) with $u(0) > 0$ and $v(0) > 0$ approaches $\boldsymbol{E}_3$ as $t \to \infty$.*

Proof. We prove only the first statement; the remaining two assertions can be proved similarly. By Lemma 2.1, the function

$$V(u, v) = \frac{1}{\rho_1}(u - 1 - \log u) + \frac{1}{\rho_2}(2 - \alpha)v$$

is a strict Lyapunov function for the system (2.1) in $(0, \infty) \times [0, \infty)$. Hence, by Lemma 4.3, the function

$$W(u_1, \ldots, u_n, v_1, \ldots, v_n) = \sum_{i=1}^{n} V(u_i, v_i)$$

is a strict Lyapunov function for the system (3.1) in $(0, \infty)^n \times [0, \infty)$, i.e., $W > 0$ on $(0, \infty)^n \times [0, \infty) \setminus \{\boldsymbol{E}_1\}$, $W(\boldsymbol{E}_1) = 0$, $\dot{W} < 0$ on $(0, \infty)^n \times [0, \infty)^n \setminus \{\boldsymbol{E}_1\}$ and $\dot{W}(\boldsymbol{E}_1) = 0$. If we choose an arbitrary $M > 0$, it follows from the definitions of V and W that $\Omega(M) = \{x \in (0, \infty)^n \times [0, \infty)^n; W(x) \leq M\}$ is a compact subset of $\mathbb{R}^{2n}$. Since W is nonincreasing along the trajectories of (3.1), $\Omega(M)$ is a positively invariant region for this system, and according to LaSalle's invariance principle, each solution starting in $\Omega(M)$ approaches $\boldsymbol{E}_1$ as $t \to \infty$ (see e.g. Lemma 6.11 and Theorem 6.14 in Teschl (2012)). Thus, if we choose $M \geq W(u(0), v(0))$, we see that the solution with initial conditions $u(0) > 0$ and $v(0) \geq 0$ approaches $\boldsymbol{E}_1$ as $t \to \infty$. □

5 Existence of heterogeneous stationary states

In all cases except $\alpha, \beta > 1$, we know from Theorem 4.5 that all solutions with positive initial values are attracted to one of the three homogeneous stationary states $\boldsymbol{E_1}$, $\boldsymbol{E_2}$, $\boldsymbol{E_3}$. In particular, there are no heterogeneous stationary states in the positive orthant. It remains to settle the case $\alpha, \beta > 1$, which leads to a much more interesting dynamics. We will see that the system (3.1) might possess a large number of heterogeneous stationary states, some of which are asymptotically stable.

The next theorem provides some basic information about the possible stationary states; in particular, it rules out the existence of heterogeneous stationary states on the boundary of the positive orthant.

Theorem 5.1. *Let $(u_1, v_1, \dots, u_n, v_n)$ be a nonnegative stationary state of* (3.1).

- *If $\rho_1 > 0$, then $u_1, \dots, u_n$ are contained in the interval* $[0, 1]$. *Similarly, if $\rho_2 > 0$, then $v_1, \dots, v_n$ are contained in the interval* $[0, 1]$.
- *If $d_1 > 0$ and there exists $i \in V$ with $u_i = 0$, then $u_1 = \dots = u_n = 0$. Similarly, if $d_2 > 0$ and there exists $i \in V$ with $v_i = 0$, then $v_1 = \dots = v_n = 0$.*

Proof. Each stationary state $(u_1, v_1, \dots, u_n, v_n)$ of the system (3.1) satisfies

$$\begin{aligned} 0 &= d_1 \sum_{j \in N(i)} (u_j - u_i) + \rho_1 u_i (1 - u_i - \alpha v_i), \qquad i \in V, \\ 0 &= d_2 \sum_{j \in N(i)} (v_j - v_i) + \rho_2 v_i (1 - v_i - \beta u_i), \qquad i \in V. \end{aligned} \tag{5.1}$$

Suppose first that $\rho_1 > 0$ and $d_1 > 0$. If $i \in V$ is an arbitrary vertex and $u_i + \alpha v_i > 1$, then the first equation in (5.1) implies that i has a neighbor $j \in N(i)$ such that $u_j > u_i$. Thus, if we choose a vertex $i \in V$ such that $u_i = \max\{u_1, \dots, u_n\}$, then necessarily $u_i + \alpha v_i \le 1$. Consequently, $u_i \le 1$, and the definition of i implies that $0 \le u_1, \dots, u_n \le 1$. On the other hand, if $d_1 = 0$, then either $u_i = 0$ or $u_i + \alpha v_i = 1$ for all $i \in V$, and therefore $0 \le u_i \le 1$. In a similar way, it is easy to show that $0 \le v_1, \dots, v_n \le 1$.

If $d_1 > 0$ and $u_i = 0$, then the first equation in (5.1) implies that $\sum_{j \in N(i)} u_j = 0$, i.e., the values of the stationary solution in all neighbors of i vanish. Since G is connected, it follows that $u_1 = \dots = u_n = 0$. The corresponding statement for $v_1, \dots, v_n$ can be proved similarly. □

Throughout the rest of this section, we assume that ρ_1, ρ_2, α, β and G are fixed, and we study the effect of diffusion on the existence of heterogeneous stationary states.

Our first goal is to show that if the diffusion is sufficiently large, there are no heterogeneous stationary states, and all solutions with nonnegative initial conditions tend to a homogeneous stationary state. Let us begin with a few preliminaries.

Suppose we wish to compare solutions of a system

$$x'(t) = F(x(t)), \tag{5.2}$$

where $F : \mathbb{R}^n \to \mathbb{R}^n$ is continuously differentiable and $F(0) = 0$, with solutions of a perturbed system

$$y'(t) = F(y(t)) + H(t), \tag{5.3}$$

where $H : \mathbb{R} \to \mathbb{R}^n$ is continuous. Let $t \mapsto x(t, t_0, x_0)$ be the solution of the unperturbed system (5.2) passing through (t_0, x_0), and let $t \mapsto \Phi(t, t_0, x_0)$ be the solution of the so-called variational system

$$z'(t) = F_x(x(t, t_0, x_0))z(t), \quad z(t_0) = I. \tag{5.4}$$

Then the following result, which is a special case of Theorem 4 in Brauer (1967), provides a relation between solutions of the perturbed and unperturbed systems.

Theorem 5.2. *If y is a solution of the perturbed system* (5.3) *and*

$$\lim_{t \to \infty} \int_t^\infty \Phi(t, s, y(s)) H(s) \, \mathrm{d}s = 0, \tag{5.5}$$

then there exists a solution x of the unperturbed system (5.2) *such that* $\lim_{t \to \infty}(x(t) - y(t)) = 0$.

Recalling that L denotes the Laplacian matrix of G, consider the bilinear form $\langle \cdot, \cdot \rangle_L : \mathbb{R}^n \times \mathbb{R}^n \to \mathbb{R}$ given by

$$\langle x, y \rangle_L = \langle x, Ly \rangle,$$

(as before, $\langle \cdot, \cdot \rangle$ denotes the standard inner product in $\mathbb{R}^n$). Since L is symmetric and positive semidefinite (see Lemma 4.3 in Bapat (2010)), it follows that $\langle \cdot, \cdot \rangle_L$ has the same properties. Thus, we have the Cauchy-Schwarz inequality

$$|\langle x, y \rangle_L| \le \sqrt{\langle x, x \rangle_L} \sqrt{\langle y, y \rangle_L} \quad \text{for all } x, y \in \mathbb{R}^n, \tag{5.6}$$

and the function $\|\cdot\|_L : \mathbb{R}^n \to [0,\infty)$ given by

$$\|x\|_L = \sqrt{\langle x,x\rangle_L} = \sqrt{\langle x, Lx\rangle} \tag{5.7}$$

is a seminorm on $\mathbb{R}^n$. Being a symmetric matrix, L has an orthonormal system of eigenvectors $\phi_1,\dots,\phi_n$, with the corresponding eigenvalues $0=\lambda_1<\lambda_2\le\lambda_3\le\cdots\le\lambda_n$. Each vector $x\in\mathbb{R}^n$ can be written in the form

$$x=\sum_{i=1}^n \langle x,\phi_i\rangle\phi_i, \tag{5.8}$$

and therefore

$$\|x\|_L^2 = \langle x, Lx\rangle = \left\langle \sum_{i=1}^n \langle x,\phi_i\rangle\phi_i, \sum_{i=2}^n \langle x,\phi_i\rangle\lambda_i\phi_i \right\rangle = \sum_{i=2}^n \langle x,\phi_i\rangle^2\lambda_i, \tag{5.9}$$

$$\|Lx\|^2 = \sum_{i=2}^n \langle x,\phi_i\rangle^2\lambda_i^2 \ge \lambda_2 \sum_{i=2}^n \langle x,\phi_i\rangle^2\lambda_i = \lambda_2\|x\|_L^2. \tag{5.10}$$

In particular, (5.9) implies that $\|x\|_L=0$ if and only if x is a multiple of $\phi_1=\frac{1}{\sqrt{n}}(1,\dots,1)$. The same fact follows also from the well-known identity (see again Lemma 4.3 in Bapat (2010))

$$\|x\|_L^2 = \langle x,x\rangle_L = \langle x, Lx\rangle = \sum_{\{i,j\}\in E} (x_i-x_j)^2. \tag{5.11}$$

Finally, for each $x\in\mathbb{R}^n$, let $\overline{x}=\frac{1}{n}\sum_{i=1}^n x_i$ and let $x^\perp=\langle x,\phi_1\rangle\phi_1=(\overline{x},\dots,\overline{x})$ be the orthogonal projection of x into the direction of ϕ_1. With the help of (5.10), we get

$$\lambda_2\|x-x^\perp\|^2 = \lambda_2\left\|\sum_{i=2}^n \langle x,\phi_i\rangle\phi_i\right\| = \lambda_2\sum_{i=2}^n \langle x,\phi_i\rangle^2 \le \sum_{i=2}^n \langle x,\phi_i\rangle^2\lambda_i = \|x\|_L^2, \tag{5.12}$$

or equivalently

$$\|x-x^\perp\| \le \frac{1}{\sqrt{\lambda_2}}\|x\|_L. \tag{5.13}$$

This inequality was already obtained (using a different method) by Stehlík and Vaněk (2017, Lemma 2.1), where it is referred to as the discrete Poincaré inequality.

We are now ready to prove the promised result. The proof is somewhat lengthy, and has two main parts: First, we prove that if the diffusion is sufficiently large, then each solution $(u(t),v(t))$ tends to the spatially homogeneous function $(u^\perp(t),v^\perp(t))$; this part is inspired by a similar result for partial differential equations from Conway et al. (1978, Theorem 3.1). Second, we will show that $(u^\perp(t),v^\perp(t))$ tends to a homogeneous stationary state by using Theorem 5.2 and comparing $(\overline{u}(t),\overline{v}(t))$ with a solution of the classical Lotka-Volterra system.

Theorem 5.3. *For each $\rho_1,\rho_2>0$, $\alpha,\beta>0$, and graph G, there exists a $D\ge0$ such that if $\min(d_1,d_2)>D$, then all solutions of (3.1) with nonnegative initial conditions tend to a homogeneous stationary state. In particular, (3.1) has no heterogeneous stationary state with nonnegative components.*

Proof. Suppose that $\Omega=[0,R]^{2n}$ with $R\ge1$. According to Corollary 3.4, a solution of (3.1) with initial conditions $(u(0),v(0))\in\Omega$ never leaves Ω. Given such a solution $u,v:[0,\infty)\to\Omega$, we consider the function

$$\ell(t)=\frac{1}{2}\left(\sum_{\{i,j\}\in E}(u_i(t)-u_j(t))^2+\sum_{\{i,j\}\in E}(v_i(t)-v_j(t))^2\right)=\frac{1}{2}\left(\langle u(t),u(t)\rangle_L+\langle v(t),v(t)\rangle_L\right)$$

and calculate its derivative with the help of (3.3):

$$\begin{aligned}
\ell'(t) &= \langle u'(t),u(t)\rangle_L+\langle v'(t),v(t)\rangle_L\\
&= \langle -d_1Lu(t)+\rho_1f_1(u(t),v(t)),u(t)\rangle_L+\langle -d_2Lv(t)+\rho_2f_2(u(t),v(t)),v(t)\rangle_L\\
&= -d_1\langle Lu(t),u(t)\rangle_L-d_2\langle Lv(t),v(t)\rangle_L+\langle \rho_1f_1(u(t),v(t)),u(t)\rangle_L+\langle \rho_2f_2(u(t),v(t)),v(t)\rangle_L.
\end{aligned}$$

According to (5.10), we have

$$-d_1\langle Lu(t), u(t)\rangle_L - d_2\langle Lv(t), v(t)\rangle_L = -d_1\|Lu(t)\|^2 - d_2\|Lv(t)\|^2 \le -d_1\lambda_2\|u(t)\|_L^2 - d_2\lambda_2\|v(t)\|_L^2.$$

Using the Cauchy-Schwarz inequality (5.6), we get

$$\begin{aligned}&\langle \rho_1 f_1(u(t), v(t)), u(t)\rangle_L + \langle \rho_2 f_2(u(t), v(t)), v(t)\rangle_L\\ &\le \|\rho_1 f_1(u(t), v(t))\|_L\|u(t)\|_L + \|\rho_2 f_2(u(t), v(t))\|_L\|v(t)\|_L.\end{aligned}$$

Next, using (5.11) and recalling the definition of f_1, f_2 from (3.4), we observe that

$$\|\rho_k f_k(u(t), v(t))\|_L = \sqrt{\sum_{\{i,j\}\in E}(h_k(u_i(t), v_i(t)) - h_k(u_j(t), v_j(t)))^2}, \quad k \in \{1, 2\},$$

where $h_1(x, y) = \rho_1 x(1 - x - \alpha y)$ and $h_2(x, y) = \rho_2 y(1 - \beta x - y)$. The mean value theorem yields the estimate

$$|h_k(u_i(t), v_i(t)) - h_k(u_j(t), v_j(t))| \le M_k(R)\sqrt{(u_i(t) - u_j(t))^2 + (v_i(t) - v_j(t))^2},$$

where

$$M_k(R) = \sup_{(x,y)\in\Omega}\|\nabla h_k(x, y)\|, \quad k \in \{1, 2\}.$$

Consequently,

$$\|\rho_k f_k(u(t), v(t))\|_L \le M_k(R)\sqrt{\sum_{\{i,j\}\in E}((u_i(t) - u_j(t))^2 + (v_i(t) - v_j(t))^2)}.$$

Finally, using the subadditivity of the square root and the identity (5.11), we get

$$\|\rho_k f_k(u(t), v(t))\|_L \le M_k(R)(\|u(t)\|_L + \|v(t)\|_L).$$

By combining all of the previous estimates, we get

$$\begin{aligned}\ell'(t) \le& - d_1\lambda_2\|u(t)\|_L^2 - d_2\lambda_2\|v(t)\|_L^2\\ &+ M_1(R)(\|u(t)\|_L + \|v(t)\|_L)\|u(t)\|_L + M_2(R)(\|u(t)\|_L + \|v(t)\|_L)\|v(t)\|_L\\ \le& - \lambda_2\min(d_1, d_2)(\|u(t)\|_L^2 + \|v(t)\|_L^2) + 2\max(\|u(t)\|_L, \|v(t)\|_L)(M_1(R)\|u(t)\|_L + M_2(R)\|v(t)\|_L)\\ \le& - \lambda_2\min(d_1, d_2)(\|u(t)\|_L^2 + \|v(t)\|_L^2) + 2\max(\|u(t)\|_L^2, \|v(t)\|_L^2)(M_1(R) + M_2(R))\\ \le&(\|u(t)\|_L^2 + \|v(t)\|_L^2)(-\lambda_2\min(d_1, d_2) + 2(M_1(R) + M_2(R)))\\ =&2\ell(t)(-\lambda_2\min(d_1, d_2) + 2(M_1(R) + M_2(R))).\end{aligned}$$

Observe that

$$M_k(R) \le M(R) := \sup_{(x,y)\in\Omega}\|J(x, y)\|, \quad k \in \{1, 2\},$$

where J is the Jacobian matrix given by (2.4), and therefore

$$0 \le \ell(t) \le \ell(0)\exp(2(-\lambda_2\min(d_1, d_2) + 4M(R))t), \quad t \ge 0. \tag{5.14}$$

Assume that

$$\min(d_1, d_2) > \frac{4M(R)}{\lambda_2}. \tag{5.15}$$

Then $\lim_{t\to\infty}\ell(t) = 0$, which already shows that (3.1) has no heterogeneous stationary states in Ω (the corresponding function ℓ would be constant and positive).

According to the discrete Poincaré inequality (5.13), we have

$$\|u(t) - u^\perp(t)\|^2 + \|v(t) - v^\perp(t)\|^2 \le \frac{1}{\lambda_2}(\|u(t)\|_L^2 + \|v(t)\|_L^2) = \frac{2}{\lambda_2}\ell(t), \tag{5.16}$$

and therefore

$$\lim_{t\to\infty}(u(t)-u^{\perp}(t))=0, \qquad \lim_{t\to\infty}(v(t)-v^{\perp}(t))=0. \tag{5.17}$$

To obtain more information about the asymptotic behavior of $u^{\perp}(t)$ and $v^{\perp}(t)$, it suffices to analyze the behavior of $\overline{u}(t)=\frac{1}{n}\sum_{i=1}^{n}u_i(t)$ and $\overline{v}(t)=\frac{1}{n}\sum_{i=1}^{n}v_i(t)$. Since $\sum_{i=1}^{n}\sum_{j\in N(i)}(u_j(t)-u_i(t))=0$ and $\sum_{i=1}^{n}\sum_{j\in N(i)}(v_j(t)-v_i(t))=0$, summation of equations (3.1) over all $i\in\{1,\ldots,n\}$ and subsequent multiplication by $\frac{1}{n}$ yields the system

$$\overline{u}'(t)=\frac{1}{n}\sum_{i=1}^{n}h_1(u_i(t),v_i(t)), \qquad \overline{v}'(t)=\frac{1}{n}\sum_{i=1}^{n}h_2(u_i(t),v_i(t)).$$

For each $k\in\{1,2\}$, we can write

$$\frac{1}{n}\sum_{i=1}^{n}h_k(u_i(t),v_i(t))=h_k(\overline{u}(t),\overline{v}(t))+\frac{1}{n}\sum_{i=1}^{n}\left(h_k(u_i(t),v_i(t))-h_k(\overline{u}(t),\overline{v}(t))\right).$$

Hence, the functions $\overline{u}$, $\overline{v}$ are solutions of the system

$$(\overline{u}'(t),\overline{v}'(t))=F(\overline{u}(t),\overline{v}(t))+H(t), \tag{5.18}$$

where

$$F_k(x,y)=h_k(x,y), \qquad H_k(t)=\frac{1}{n}\sum_{i=1}^{n}\left(h_k(u_i(t),v_i(t))-h_k(\overline{u}(t),\overline{v}(t))\right), \quad k\in\{1,2\}.$$

The system (5.3) can be viewed as a perturbation of the classical Lotka-Volterra system

$$(U'(t),V'(t))=F(U(t),V(t)). \tag{5.19}$$

We want to apply Theorem 5.2 and show that for $y(t)=(\overline{u}(t),\overline{v}(t))$, there exists a solution $x(t)=(U(t),V(t))$ of (5.19) such that $\lim_{t\to\infty}(x(t)-y(t))=0$. To see that the assumption (5.5) holds, we need to estimate the size of the perturbation H and the solution Φ of the variational system.

With the help of the mean value theorem, the Cauchy-Schwarz inequality, and (5.16), we get

$$|H_k(s)|\le\frac{1}{n}\sum_{i=1}^{n}|h_k(u_i(s),v_i(s))-h_k(\overline{u}(s),\overline{v}(s))|$$

$$\le\frac{1}{n}M_k(R)\sum_{i=1}^{n}\sqrt{(u_i(s)-\overline{u}(s))^2+(v_i(s)-\overline{v}(s))^2}\le\frac{1}{n}M_k(R)\sqrt{n}\sqrt{\sum_{i=1}^{n}(u_i(s)-\overline{u}(s))^2+(v_i(s)-\overline{v}(s))^2}$$

$$=\frac{1}{\sqrt{n}}M_k(R)\sqrt{\|u(s)-u^{\perp}(s)\|^2+\|v(s)-v^{\perp}(s)\|^2}\le\frac{1}{\sqrt{n}}M_k(R)\sqrt{\frac{2}{\lambda_2}\ell(s)}, \quad k\in\{1,2\}.$$

Hence, using (5.14), we see there exists a number $k(R)>0$ such that

$$\|H(s)\|\le k(R)\exp\left((-\lambda_2\min(d_1,d_2)+4M(R))s\right).$$

Next, we recall that $t\mapsto\Phi(t,s,y(s))$ is a solution of the variational system

$$z'(t)=J(x(t,s,y(s)))z(t), \quad z(s)=I, \tag{5.20}$$

where J is the Jacobian matrix from (2.4). Since the solution $y(t)=(\overline{u}(t),\overline{v}(t))$ never leaves the compact set Ω, the solution $t\mapsto x(t,s,y(s))$ of the unperturbed system (5.19) has the same property, and therefore

$$\|J(x(t,s,y(s)))\|\le M(R).$$

Hence, it follows from (5.20) that

$$\|\Phi(t,s,y(s))\| \leq \exp\left(M(R)(s-t)\right), \quad s \geq t.$$

By combining the previous estimates, we get

$$\|\Phi(t,s,y(s))\| \cdot \|H(s)\| \leq k(R)e^{-M(R)t}e^{as},$$

where $a = -\lambda_2 \min(d_1, d_2) + 5M(R)$. If $a < 0$, which happens if

$$\min(d_1, d_2) > D(R) := \frac{5M(R)}{\lambda_2},$$

then

$$\left\| \int_t^\infty \Phi(t,s,y(s))H(s)\,\mathrm{d}s \right\| \leq k(R)e^{-M(R)t} \int_t^\infty e^{as}\,\mathrm{d}s = k(R)e^{-M(R)t}\frac{-e^{at}}{a},$$

and hence the assumption (5.5) holds. Thus, there exists a solution $x(t) = (U(t), V(t))$ of the unperturbed system (5.19) such that

$$\lim_{t\to\infty} (\overline{u}(t) - U(t)) = 0, \qquad \lim_{t\to\infty} (\overline{v}(t) - V(t)) = 0. \tag{5.21}$$

Recall that $(U(t), V(t))$ is a solution of the classical Lotka-Volterra system (2.1). Although Theorem 5.2 does not ensure that $U(0)$, $V(0) \geq 0$, it follows from (5.21) that the distance of $(U(t), V(t))$ from the 1st quadrant approaches zero. This happens only for initial conditions from the 1st, 2nd or 4th quadrant, and such solutions necessarily satisfy $\lim_{t\to\infty}(U(t), V(t)) = E_k$ for a certain $k \in \{0, 1, 2, 3\}$.

Returning to (5.17) and recalling that all components of $u^\perp(t)$ and $v^\perp(t)$ are equal to $\overline{u}(t)$ and $\overline{v}(t)$, respectively, we see that

$$\lim_{t\to\infty} (u_i(t) - U(t)) = 0, \qquad \lim_{t\to\infty} (v_i(t) - V(t)) = 0, \qquad i \in \{1, \ldots, n\}.$$

This means that $\lim_{t\to\infty}(u_i(t), v_i(t)) = E_k$ for all $i \in \{1, \ldots, n\}$.

To sum up, we have proved that if $\min(d_1, d_2) > D(R)$, then each solution of (3.1) with initial conditions in $[0, R]^{2n}$ tends to a homogeneous stationary state. Now, let $D = D(1)$. Observe that $M(R)$ and therefore also $D(R)$ depend continuously on R. Thus, if $\min(d_1, d_2) > D$, one can find an $R > 1$ such that $\min(d_1, d_2) > D(R)$. Now, according to Corollary 3.4, each solution of (3.1) with nonnegative initial conditions will at a certain time enter the invariant region $[0, R]^{2n}$. Since $\min(d_1, d_2) > D(R)$, we know from the previous part of the proof that the solution will approach a homogeneous stationary state. □

We now proceed to the opposite case when the diffusion is small. If $d_1 = d_2 = 0$ and $\rho_1, \rho_2 > 0$, the situation is simple: (5.1) holds if and only if each pair (u_i, v_i) coincides with one of the four points E_0, E_1, E_2, E_3 introduced in Section 2. Hence, all stationary points of the system (3.1) have the form

$$\boldsymbol{E}_\sigma = (E_{\sigma(1)}, \ldots, E_{\sigma(n)}), \tag{5.22}$$

where $\sigma = (\sigma(1), \ldots, \sigma(n)) \in \{0, 1, 2, 3\}^n$. If $\alpha > 1$ and $\beta > 1$, then all four points E_0, E_1, E_2, E_3 have nonnegative components, and hence the system (3.1) has 4^n nonnegative stationary states; four of them are homogeneous (namely $\boldsymbol{E}_0$, $\boldsymbol{E}_1$, $\boldsymbol{E}_2$, $\boldsymbol{E}_3$), and the remaining $4^n - 4$ are heterogeneous.

However, we are primarily interested in what happens if $d_1, d_2 > 0$. It is reasonable to expect that if d_1, d_2 are small, the system (3.1) will possess 4^n stationary solutions close to $\boldsymbol{E}_\sigma$, $\sigma \in \{0, 1, 2, 3\}^n$; this is the content of the next lemma.

Lemma 5.4. *For each $\rho_1, \rho_2 > 0$, $\alpha, \beta > 1$ and graph G, there exist disjoint sets $U(\boldsymbol{E}_\sigma) \subset \mathbb{R}^{2n}$, $\sigma \in \{0, 1, 2, 3\}^n$, an $\varepsilon > 0$, and smooth functions $F_\sigma : [0, \varepsilon] \times [0, \varepsilon] \to U(\boldsymbol{E}_\sigma)$, $\sigma \in \{0, 1, 2, 3\}^n$, with the following properties:*

- *$F_\sigma(0, 0) = \boldsymbol{E}_\sigma$ for each $\sigma \in \{0, 1, 2, 3\}^n$.*

- *If $\sigma \in \{0,1,2,3\}^n$ and $d_1, d_2 \in [0, \varepsilon]$, then $F_\sigma(d_1, d_2)$ is a stationary state of the system* (3.1)*. This state is asymptotically stable if and only if $\sigma \in \{1,2\}^n$, and unstable otherwise.*

Proof. The equilibria of the system (3.1) correspond to solutions of the equation

$$H(d_1, d_2, u_1, v_1, \ldots, u_n, v_n) = 0, \tag{5.23}$$

where $H : \mathbb{R}^{2n+2} \to \mathbb{R}^{2n}$ is given by

$$H(d_1, d_2, u_1, v_1, \ldots, u_n, v_n) = \begin{pmatrix} -d_1 L & 0 \\ 0 & -d_2 L \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix} + \begin{pmatrix} \rho_1 f_1(u,v) \\ \rho_2 f_2(u,v) \end{pmatrix}, \tag{5.24}$$

and $f_1, f_2 : \mathbb{R}^{2n} \to \mathbb{R}^n$ are defined in (3.4). Choose an arbitrary $\sigma \in \{0,1,2,3\}^n$ and note that $H(0, 0, \boldsymbol{E}_\sigma) = 0$. The function H is infinitely differentiable, and its Jacobian matrix with respect to $(u_1, v_1, \ldots, u_n, v_n)$ is

$$\frac{\partial H}{\partial(u,v)}(d_1, d_2, u_1, v_1, \ldots, u_n, v_n) = \begin{pmatrix} -d_1 L & 0 \\ 0 & -d_2 L \end{pmatrix} + \begin{pmatrix} \rho_1 \frac{\partial f_{1,1}}{\partial u_1} & & & \rho_1 \frac{\partial f_{1,1}}{\partial v_1} & & \\ & \ddots & & & \ddots & \\ & & \rho_1 \frac{\partial f_{1,n}}{\partial u_n} & & & \rho_1 \frac{\partial f_{1,n}}{\partial v_n} \\ \rho_2 \frac{\partial f_{2,1}}{\partial u_1} & & & \rho_2 \frac{\partial f_{2,1}}{\partial v_1} & & \\ & \ddots & & & \ddots & \\ & & \rho_2 \frac{\partial f_{2,n}}{\partial u_n} & & & \rho_2 \frac{\partial f_{2,n}}{\partial v_n} \end{pmatrix},$$

where $f_{k,i}$ denotes the i-th component of f_k. When evaluated at $(d_1, d_2) = (0, 0)$, we get

$$\frac{\partial H}{\partial(u,v)}(0, 0, u_1, v_1, \ldots, u_n, v_n) = \begin{pmatrix} \rho_1 \frac{\partial f_{1,1}}{\partial u_1} & & & \rho_1 \frac{\partial f_{1,1}}{\partial v_1} & & \\ & \ddots & & & \ddots & \\ & & \rho_1 \frac{\partial f_{1,n}}{\partial u_n} & & & \rho_1 \frac{\partial f_{1,n}}{\partial v_n} \\ \rho_2 \frac{\partial f_{2,1}}{\partial u_1} & & & \rho_2 \frac{\partial f_{2,1}}{\partial v_1} & & \\ & \ddots & & & \ddots & \\ & & \rho_2 \frac{\partial f_{2,n}}{\partial u_n} & & & \rho_2 \frac{\partial f_{2,n}}{\partial v_n} \end{pmatrix}.$$

The eigenvalues of this matrix coincide with the eigenvalues of the block diagonal matrix

$$\begin{pmatrix} \rho_1 \frac{\partial f_{1,1}}{\partial u_1} & \rho_1 \frac{\partial f_{1,1}}{\partial v_1} & & & \\ \rho_2 \frac{\partial f_{2,1}}{\partial u_1} & \rho_2 \frac{\partial f_{2,1}}{\partial v_1} & & & \\ & & \ddots & & \\ & & & \rho_1 \frac{\partial f_{1,n}}{\partial u_n} & \rho_1 \frac{\partial f_{1,n}}{\partial v_n} \\ & & & \rho_2 \frac{\partial f_{2,n}}{\partial u_n} & \rho_2 \frac{\partial f_{2,n}}{\partial v_n} \end{pmatrix}. \tag{5.25}$$

For $(u_1, v_1, \ldots, u_n, v_n) = \boldsymbol{E}_\sigma$, the i-th block on the diagonal coincides with the Jacobian matrix $J(E_{\sigma(i)})$ of the classical Lotka-Volterra system (see (2.4)), which has two nonzero eigenvalues. Hence, the matrix (5.25) is regular, and therefore the Jacobian matrix $\frac{\partial H}{\partial(u,v)}(0, 0, \boldsymbol{E}_\sigma)$ is also regular. The implicit function theorem guarantees the existence of a neighborhood $U(\boldsymbol{E}_\sigma)$ of $\boldsymbol{E}_\sigma$ and an $\varepsilon_\sigma > 0$ such that if $d_1, d_2 \in [-\varepsilon_\sigma, \varepsilon_\sigma]$, there is a unique $(u,v) \in U(\boldsymbol{E}_\sigma)$ such that (5.23) holds. Denoting $F_\sigma(d_1, d_2) = (u,v)$, we obtain a smooth function $F_\sigma : [-\varepsilon_\sigma, \varepsilon_\sigma] \times [-\varepsilon_\sigma, \varepsilon_\sigma] \to U(\boldsymbol{E}_\sigma)$.

For a given pair d_1, d_2, the Jacobian matrix of the system (3.1) is (5.24). If $d_1 = d_2 = 0$ and $(u,v) = \boldsymbol{E}_\sigma$, we know that the Jacobian matrix has the same eigenvalues as the block diagonal matrix (5.25) evaluated at $\boldsymbol{E}_\sigma$. Since eigenvalues depend continuously on the matrix entries and F_σ is continuous, if d_1 and d_2 are sufficiently small, then $F_\sigma(d_1, d_2)$ will be close to $\boldsymbol{E}_\sigma$, and the Jacobian matrix at the equilibrium point $F_\sigma(d_1, d_2)$ (i.e., the matrix $\frac{\partial H}{\partial(u,v)}(d_1, d_2, F_\sigma(d_1, d_2)))$ will have the same number of eigenvalues with positive and negative real parts as the Jacobian matrix at $(0,0,\boldsymbol{E}_\sigma)$. Without loss of generality, we can assume that $\varepsilon_\sigma > 0$ was chosen so small that this property holds for all $d_1, d_2 \in [0, \varepsilon_\sigma]$. Hence, for each $d_1, d_2 \in [0, \varepsilon_\sigma]$, the equilibrium $F_\sigma(d_1, d_2)$ is asymptotically stable (or unstable) if and only if $\boldsymbol{E}_\sigma$ is stable (or unstable), which happens if and only if $\sigma \in \{1,2\}^n$ (or if $\sigma(i) \in \{0,3\}$ for at least one $i \in \{1,\dots,n\}$, respectively).

Repeating the previous process for all $\sigma \in \{0,1,2,3\}^n$, we get a collection of functions $F_\sigma : [0,\varepsilon] \times [0,\varepsilon] \to U(\boldsymbol{E}_\sigma)$ with $\varepsilon = \min\{\varepsilon_\sigma : \sigma \in \{0,1,2,3\}^n\}$. Without loss of generality, we can assume that all of the neighborhoods $U(\boldsymbol{E}_\sigma)$, $\sigma \in \{0,1,2,3\}^n$ are disjoint (since $\boldsymbol{E}_\sigma$ are distinct points, this can always be achieved by taking a sufficiently small $\varepsilon > 0$). □

The previous lemma says that if $d_1, d_2 \geq 0$ are sufficiently small, then (3.1) has 4^n stationary solutions $F_\sigma(d_1, d_2) \in \mathbb{R}^{2n}$, where $\sigma \in \{0,1,2,3\}^n$; four of them corresponding to $\sigma = (i,\dots,i)$ with $i \in \{0,1,2,3\}$ are homogeneous, while the remaining $4^n - 4$ are heterogeneous (this follows from the fact that the neighborhoods $U(\boldsymbol{E}_\sigma)$ are disjoint) and $2^n - 2$ of them are asymptotically stable.

The idea of using the implicit function theorem to study stationary states of networks consisting of weakly coupled bistable units can be found e.g. in MacKay and Sepulchre (1995). However, in the present problem, we have to be careful, since the heterogeneous equilibria need not be nonnegative. If $\sigma(i) = 3$, then $(u_i(d_1, d_2), v_i(d_1, d_2))$ is close to E_3, and therefore nonnegative. On the other hand, if $\sigma(i) \in \{0,1,2\}$, we do not a priori know whether $u_i(d_1, d_2)$ and $v_i(d_1, d_2)$ are nonnegative.

To settle this question, we will assume that $d_1 = d\delta_1$ and $d_2 = d\delta_2$, where $\delta_1, \delta_2 > 0$ are fixed, and d is a variable. In other words, the ratio of diffusion coefficients is fixed to be δ_1/δ_2, but their magnitudes are allowed to vary.

Given a connected graph G, 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 $i \in V$ as the set $N_k(i)$ consisting of all vertices whose distance from i does not exceed k. (In particular, $N_0(i) = \{i\}$ and $N_1(i) = N(i) \cup \{i\}$ for all $i \in V$.)

The next lemma provides some information about the derivatives of the components of F_σ, which will be used later to find equilibria with nonnegative components.

Lemma 5.5. *Suppose that $\alpha, \beta > 1$, $\delta_1, \delta_2 > 0$, and $F_\sigma : [0,\varepsilon] \times [0,\varepsilon] \to U(\boldsymbol{E}_\sigma)$, $\sigma \in \{0,1,2,3\}^n$, are as in the previous lemma. Let*

$$(u_1(d), \dots, u_n(d), v_1(d), \dots, v_n(d)) := F_\sigma(d\delta_1, d\delta_2) \tag{5.26}$$

for all $d \geq 0$ such that $d\delta_1, d\delta_2 \in [0,\varepsilon]$. Then the following statements hold:

- *If $i \in V$ is such that $\sigma(i) = 0$ and $\sigma(k) \neq 0$ for a certain $k \in N(i)$, then $u_i'(0) < 0$ or $v_i'(0) < 0$.*
- *Suppose that $\sigma \in \{1,2,3\}^n$ and $\ell \in \mathbb{N}$. If $i \in V$ is such that $\sigma(i) = 1$ and all vertices $k \in N_{\ell-1}(i)$ have $\sigma(k) = 1$, then*

$$v_i(0) = v_i'(0) = \cdots = v_i^{(\ell-1)}(0) = 0, \qquad v_i^{(\ell)}(0) = \frac{\delta_2 \ell}{\rho_2(\beta-1)} \sum_{j \in N(i)} v_j^{(\ell-1)}(0). \tag{5.27}$$

- *Suppose that $\sigma \in \{1,2,3\}^n$ and $\ell \in \mathbb{N}$. If $i \in V$ is such that $\sigma(i) = 2$ and all vertices $k \in N_{\ell-1}(i)$ have $\sigma(k) = 2$, then*

$$u_i(0) = u_i'(0) = \cdots = u_i^{(\ell-1)}(0) = 0, \qquad u_i^{(\ell)}(0) = \frac{\delta_1 \ell}{\rho_1(\alpha-1)} \sum_{j \in N(i)} u_j^{(\ell-1)}(0). \tag{5.28}$$

Proof. If $d \geq 0$ is such that $d\delta_1, d\delta_2 \in [0,\varepsilon]$, then $F_\sigma(d\delta_1, d\delta_2)$ is a stationary state of (3.1) with $d_1 = d\delta_1$ and $d_2 = d\delta_2$, and therefore

$$\begin{pmatrix} d\delta_1 \sum_{j \in N(i)} (u_i(d) - u_j(d)) \\ d\delta_2 \sum_{j \in N(i)} (v_i(d) - v_j(d)) \end{pmatrix} = \begin{pmatrix} h_1(u_i(d), v_i(d)) \\ h_2(u_i(d), v_i(d)) \end{pmatrix}, \quad i \in V, \tag{5.29}$$

where $h_1(x,y) = \rho_1 x(1-x-\alpha y)$ and $h_2(x,y) = \rho_2 y(1-\beta x - y)$. Differentiation with respect to d gives

$$\begin{pmatrix} \delta_1 \sum_{j\in N(i)}(u_i - u_j) + d\delta_1 \sum_{j\in N(i)}\left(u_i' - u_j'\right) \\ \delta_2 \sum_{j\in N(i)}(v_i - v_j) + d\delta_2 \sum_{j\in N(i)}\left(v_i' - v_j'\right) \end{pmatrix} = \begin{pmatrix} \frac{\partial h_1}{\partial x} u_i' + \frac{\partial h_1}{\partial y} v_i' \\ \frac{\partial h_2}{\partial x} u_i' + \frac{\partial h_2}{\partial y} v_i' \end{pmatrix}. \tag{5.30}$$

To avoid lengthy formulas, we have suppressed the arguments of all functions, but we keep in mind that u_i, u_j, v_i, v_j and their derivatives are always evaluated at d, while the derivatives of h_1, h_2 are always evaluated at $(u_i(d), v_i(d))$.

We now substitute $d = 0$; observing that $(u_i(0), v_i(0)) = E_{\sigma(i)}$, that the right-hand side of (5.30) is simply $J(E_{\sigma(i)}) \begin{pmatrix} u_i'(0) \\ v_i'(0) \end{pmatrix}$, and using the fact that $J(E_{\sigma(i)})$ is invertible, we obtain

$$\begin{pmatrix} u_i'(0) \\ v_i'(0) \end{pmatrix} = J(E_{\sigma(i)})^{-1} \begin{pmatrix} \delta_1 \sum_{j\in N(i)}(u_i(0) - u_j(0)) \\ \delta_2 \sum_{j\in N(i)}(v_i(0) - v_j(0)) \end{pmatrix}. \tag{5.31}$$

For further calculations, we need the following inverse matrices, which can be obtained from (2.4):

$$J(E_0)^{-1} = \begin{pmatrix} \frac{1}{\rho_1} & 0 \\ 0 & \frac{1}{\rho_2} \end{pmatrix}, \quad J(E_1)^{-1} = \begin{pmatrix} -\frac{1}{\rho_1} & \frac{\alpha}{\rho_2(\beta-1)} \\ 0 & \frac{1}{\rho_2(1-\beta)} \end{pmatrix}, \quad J(E_2)^{-1} = \begin{pmatrix} \frac{1}{\rho_1(1-\alpha)} & 0 \\ \frac{\beta}{\rho_1(\alpha-1)} & -\frac{1}{\rho_2} \end{pmatrix}. \tag{5.32}$$

Now, suppose that $\sigma(i) = 0$ for a certain $i \in V$ having a neighbor $k \in N(i)$ with $\sigma(k) \neq 0$. Then $(u_i(0), v_i(0)) = E_0 = (0,0)$, and $(u_k(0), v_k(0)) \in \{E_1, E_2, E_3\}$. Hence, either $u_k(0) > 0$ and therefore (5.31) combined with (5.32) yields

$$u_i'(0) = \frac{\delta_1}{\rho_1} \sum_{j\in N(i)} (u_i(0) - u_j(0)) = -\frac{\delta_1}{\rho_1} \sum_{j\in N(i)} u_j(0) \leq -\frac{\delta_1}{\rho_1} u_k(0) < 0,$$

or $v_k(0) > 0$ and therefore (5.31) combined with (5.32) yields

$$v_i'(0) = \frac{\delta_2}{\rho_2} \sum_{j\in N(i)} (v_i(0) - v_j(0)) = -\frac{\delta_2}{\rho_2} \sum_{j\in N(i)} v_j(0) \leq -\frac{\delta_2}{\rho_2} v_k(0) < 0.$$

This proves the first statement.

The second statement will be proved by induction with respect to ℓ. First, we show that it holds for $\ell = 1$. Suppose that $\sigma(i) = 1$. Then it is clear that $v_i(0) = 0$. Moreover, (5.31) combined with (5.32) yields

$$v_i'(0) = \frac{\delta_2}{\rho_2(1-\beta)} \sum_{j\in N(i)} (v_i(0) - v_j(0)) = \frac{\delta_2}{\rho_2(\beta-1)} \sum_{j\in N(i)} v_j(0).$$

Next, suppose that the second statement is valid for $\ell - 1$, and let us prove it for ℓ. Hence, we now assume that $\sigma(i) = 1$ and that all vertices $k \in N_{\ell-1}(i)$ have $\sigma(k) = 1$. By the induction hypothesis, we know that

$$v_i(0) = v_i'(0) = \cdots = v_i^{(\ell-2)}(0) = 0, \qquad v_i^{(\ell-1)}(0) = \frac{\delta_2(\ell-1)}{\rho_2(\beta-1)} \sum_{j\in N(i)} v_j^{(\ell-2)}(0).$$

If $j \in N(i)$, then $N_{\ell-2}(j)$ is a subset of $N_{\ell-1}(i)$, which contains only vertices k with $\sigma(k) = 1$. Hence, by induction hypothesis, $v_j^{(\ell-2)}(0) = 0$. Consequently,

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

We now return to (5.29), and calculate its ℓ-th derivative with respect to d. Using the Leibniz rule for higher-order derivatives of a product of two functions, we find that the ℓ-th derivative of the left-hand side of (5.29) is

$$\begin{pmatrix} d\delta_1 \sum_{j\in N(i)} \left(u_i^{(\ell)} - u_j^{(\ell)}\right) + \delta_1 \ell \sum_{j\in N(i)} \left(u_i^{(\ell-1)} - u_j^{(\ell-1)}\right) \\ d\delta_2 \sum_{j\in N(i)} \left(v_i^{(\ell)} - v_j^{(\ell)}\right) + \delta_2 \ell \sum_{j\in N(i)} \left(v_i^{(\ell-1)} - v_j^{(\ell-1)}\right) \end{pmatrix}. \tag{5.33}$$

Instead of calculating the ℓ-th derivative of the right-hand side of (5.29), it is more convenient to calculate the $(\ell-1)$-th derivative of the right-hand side of (5.30). We claim the result has the form

$$\begin{pmatrix} \frac{\partial h_1}{\partial x} u_i^{(\ell)} + \frac{\partial h_1}{\partial y} v_i^{(\ell)} + \cdots \\ \frac{\partial h_2}{\partial x} u_i^{(\ell)} + \frac{\partial h_2}{\partial y} v_i^{(\ell)} + \text{multiples of } v_i', \ldots, v_i^{(\ell-1)} \end{pmatrix}, \tag{5.34}$$

where the dots in the first component indicate terms whose values are unimportant for later calculation. The form of the second component can be verified by induction: The second component on the right-hand side of (5.30) is $\frac{\partial h_2}{\partial x} u_i' + \frac{\partial h_2}{\partial y} v_i'$, which agrees with the second component of the right-hand side in (5.34) when $\ell = 1$. To verify the induction step, it suffices to observe that $\frac{\partial^2 h_2}{\partial x^2} = 0$, and therefore

$$\begin{aligned} &\left(\frac{\partial h_2}{\partial x} u_i^{(m)} + \frac{\partial h_2}{\partial y} v_i^{(m)} + \text{multiples of } v_i', \ldots, v_i^{(m-1)}\right)' = \\ &= \frac{\partial h_2}{\partial x} u_i^{(m+1)} + \frac{\partial h_2}{\partial y} v_i^{(m+1)} + \left(\frac{\partial^2 h_2}{\partial x^2} u_i' + \frac{\partial^2 h_2}{\partial x \partial y} v_i'\right) u_i^{(m)} + \left(\frac{\partial^2 h_2}{\partial y \partial x} u_i' + \frac{\partial^2 h_2}{\partial y^2} v_i'\right) v_i^{(m)} \\ &+ \text{multiples of } v_i', \ldots, v_i^{(m)} = \frac{\partial h_2}{\partial x} u_i^{(m+1)} + \frac{\partial h_2}{\partial y} v_i^{(m+1)} + \text{multiples of } v_i', \ldots, v_i^{(m)}. \end{aligned}$$

After equating (5.33) and (5.34), letting $d = 0$ and recalling that $v_i(0) = v_i'(0) = \cdots = v_i^{(\ell-1)}(0) = 0$, we get

$$\begin{pmatrix} \delta_1 \ell \sum_{j\in N(i)} \left(u_i^{(\ell-1)}(0) - u_j^{(\ell-1)}(0)\right) \\ -\delta_2 \ell \sum_{j\in N(i)} v_j^{(\ell-1)}(0) \end{pmatrix} = \begin{pmatrix} \frac{\partial h_1}{\partial x}(E_1) u_i^{(\ell)}(0) + \frac{\partial h_1}{\partial y}(E_1) v_i^{(\ell)}(0) + \cdots \\ \frac{\partial h_2}{\partial x}(E_1) u_i^{(\ell)}(0) + \frac{\partial h_2}{\partial y}(E_1) v_i^{(\ell)}(0) \end{pmatrix},$$

or equivalently

$$\begin{pmatrix} \delta_1 \ell \sum_{j\in N(i)} \left(u_i^{(\ell-1)}(0) - u_j^{(\ell-1)}(0)\right) \\ -\delta_2 \ell \sum_{j\in N(i)} v_j^{(\ell-1)}(0) \end{pmatrix} = J(E_1) \begin{pmatrix} u_i^{(\ell)}(0) \\ v_i^{(\ell)}(0) \end{pmatrix} + \begin{pmatrix} \cdots \\ 0 \end{pmatrix}.$$

Using the formula for $J(E_1)^{-1}$ from (5.32), we obtain

$$\begin{pmatrix} u_i^{(\ell)}(0) \\ v_i^{(\ell)}(0) \end{pmatrix} = \begin{pmatrix} -\frac{1}{\rho_1} & \frac{\alpha}{\rho_2(\beta-1)} \\ 0 & \frac{1}{\rho_2(1-\beta)} \end{pmatrix} \left[\begin{pmatrix} \delta_1 \ell \sum_{j\in N(i)} \left(u_i^{(\ell-1)}(0) - u_j^{(\ell-1)}(0)\right) \\ -\delta_2 \ell \sum_{j\in N(i)} v_j^{(\ell-1)}(0) \end{pmatrix} - \begin{pmatrix} \cdots \\ 0 \end{pmatrix}\right],$$

which finally gives the relation

$$v_i^{(\ell)}(0) = \frac{\delta_2 \ell}{\rho_2(\beta-1)} \sum_{j\in N(i)} v_j^{(\ell-1)}(0).$$

To prove the third statement, it suffices to interchange the roles of u and v, α and β, ρ_1 and ρ_2, δ_1 and δ_2. □

We are now able to determine which of the stationary states $F_\sigma(d\delta_1, d\delta_2)$ have nonnegative components for all sufficiently small $d > 0$. If $\sigma = (i, \ldots, i)$ for some $i \in \{0, 1, 2, 3\}$, then $F_\sigma(d\delta_1, d\delta_2) = \boldsymbol{E}_i$. Thus, it suffices to consider only n-tuples $\sigma \in \{0, 1, 2, 3\}^n$ whose components do not all coincide.

Theorem 5.6. *Consider a graph G and assume that $\alpha, \beta > 1$, $\delta_1, \delta_2 > 0$, and $F_\sigma : [0, \varepsilon] \times [0, \varepsilon] \to U(\boldsymbol{E}_\sigma)$, $\sigma \in \{0, 1, 2, 3\}^n$, are as in Lemma 5.4. There exists a $\Delta > 0$ with the following properties:*

- *Suppose that $\sigma \in \{0, 1, 2, 3\}^n$, $\sigma \neq (0, \ldots, 0)$, and there exists an $i \in V$ with $\sigma(i) = 0$. Then at least one component of $F_\sigma(d\delta_1, d\delta_2)$ is negative for all $d \in (0, \Delta]$.*
- *Suppose that $\sigma \in \{1, 2, 3\}^n$ and not all components of σ coincide. Then for each $d \in (0, \Delta]$, $F_\sigma(d\delta_1, d\delta_2)$ is a heterogeneous stationary state of (3.1), where $d_1 = d\delta_1$ and $d_2 = d\delta_2$, with positive components.*

Proof. Consider a $\sigma \in \{0,1,2,3\}^n$. As in Lemma 5.5, let

$$(u_1(d), \dots, u_n(d), v_1(d), \dots, v_n(d)) := F_\sigma(d\delta_1, d\delta_2)$$

for all $d \geq 0$ such that $d\delta_1, d\delta_2 \in [0, \varepsilon]$.

To prove the first claim, suppose that $\sigma \neq (0, \dots, 0)$ and that there exists an $i \in V$ with $\sigma(i) = 0$, i.e., $(u_i(0), v_i(0)) = E_0 = (0,0)$. Without loss of generality, we can assume that i was chosen in such a way that it has a neighbor $k \in N(i)$ with $\sigma(k) \neq 0$. Then Lemma 5.5 implies that $u_i'(0) < 0$ or $v_i'(0) < 0$. In both cases, we see that at least one component of $(u_i(d), v_i(d))$ is negative for all sufficiently small $d > 0$.

For the proof of the second claim, assume that $\sigma \in \{1,2,3\}^n$ and not all components of σ coincide. We need to show that $F_\sigma(d\delta_1, d\delta_2)$ has positive components whenever $d > 0$ is sufficiently small. Choose an arbitrary $i \in V$.

If $\sigma(i) = 1$, then $(u_i(0), v_i(0)) = E_1 = (1,0)$, and it suffices to show that $v_i(d)$ is positive for all sufficiently small $d > 0$. Take the unique $\ell \in \mathbb{N}$ such that all vertices $k \in N_{\ell-1}(i)$ have $\sigma(k) = 1$, but at least one vertex $k \in N_\ell(i)$ has $\sigma(k) \in \{2,3\}$. According to Lemma 5.5, we have

$$v_i(0) = v_i'(0) = \dots = v_i^{(\ell-1)}(0) = 0, \qquad v_i^{(\ell)}(0) = \frac{\delta_2 \ell}{\rho_2(\beta-1)} \sum_{j \in N(i)} v_j^{(\ell-1)}(0).$$

To obtain an alternative formula for $v_i^{(\ell)}(0)$, observe that for each $j \in N(i)$, $N_{\ell-2}(j)$ is a subset of $N_{\ell-1}(i)$, and therefore contains only vertices k with $\sigma(k) = 1$. Hence, by Lemma 5.5, we have $v_j^{(\ell-1)}(0) = \frac{\delta_2(\ell-1)}{\rho_2(\beta-1)} \sum_{k \in N(j)} v_k^{(\ell-2)}(0)$, and consequently

$$v_i^{(\ell)}(0) = \frac{\delta_2^2 \ell(\ell-1)}{\rho_2^2(\beta-1)^2} \sum_{j \in N(i)} \sum_{k \in N(j)} v_k^{(\ell-2)}(0).$$

For each $k \in N(j)$ appearing in the inner sum, $N_{\ell-3}(k)$ is a subset of $N_{\ell-1}(i)$, and therefore contains only vertices k with $\sigma(k) = 1$. Thus, we can use Lemma 5.5 to express $v_k^{(\ell-2)}(0)$ as a sum over $N(k)$, and the double sum becomes a triple sum. By repeating this process, we finally arrive at the formula

$$v_i^{(\ell)}(0) = \frac{\delta_2^\ell \ell!}{\rho_2^\ell(\beta-1)^\ell} \sum_{i_1 \in N(i)} \sum_{i_2 \in N(i_1)} \cdots \sum_{i_\ell \in N(i_{\ell-1})} v_{i_\ell}(0).$$

Recall that at least one vertex $k \in N_\ell(i)$ has $\sigma(k) \in \{2,3\}$ and therefore $v_k(0) > 0$, from which we see that the ℓ-fold sum is necessarily positive. Therefore $v_i^{(\ell)}(0) > 0$, which proves that $v_i(d)$ is positive for all sufficiently small $d > 0$.

If $\sigma(i) = 2$, then $(u_i(0), v_i(0)) = E_2 = (0,1)$, and it suffices to show that $u_i(d)$ is positive for all sufficiently small $d > 0$. The proof is completely analogous to the previous part, and we omit it.

If $\sigma(i) = 3$, then $(u_i(0), v_i(0)) = E_3 > (0,0)$. By continuity, $(u_i(d), v_i(d)) > (0,0)$ for all sufficiently small $d > 0$. ☐

We see that if $\alpha, \beta > 1$, $d_1 = d\delta_1$, $d_2 = d\delta_2$, and $d \geq 0$ is sufficiently small, then (3.1) has $3^n - 3$ heterogeneous stationary states with nonnegative components. Moreover, Lemma 5.4 implies that $2^n - 2$ of them are asymptotically stable. The biological interpretation is as follows: For each of the n patches, we can choose among the following three possibilites:

1. The patch will be dominated by species 1; species 2 will survive, but its population will be negligible.

2. The patch will be dominated by species 2; species 1 will survive, but its population will be negligible.

3. Both species will coexist in the given patch.

For each of the 3^n choices, it is possible to find a corresponding stationary state of (3.1), provided that d_1 and d_2 are sufficiently small. Moreover, this state will be stable if and only if we restrict our choices to the first two possibilities.

Example 5.7. As a simple illustration, we consider a graph with two vertices connected by an edge. We take $\rho_1 = \rho_2 = 1$, $\alpha = \beta = 2$, and $\delta_1 = \delta_2 = 1$, i.e., $d_1 = d_2 = d$.

If $d = 0$, there are two stable heterogeneous equilibria $(E_1, E_2) = (1, 0, 0, 1)$ and $(E_2, E_1) = (0, 1, 1, 0)$. Figure 3 shows a numerically calculated solution of (3.1) approaching the latter stationary state. The initial conditions are $u_1(0) = 0.1$, $v_1(0) = 0.7$, $u_2(0) = 0.9$, $v_2(0) = 0.3$. We see that species 1 becomes extinct at vertex 1, and species 2 becomes extinct at vertex 2.

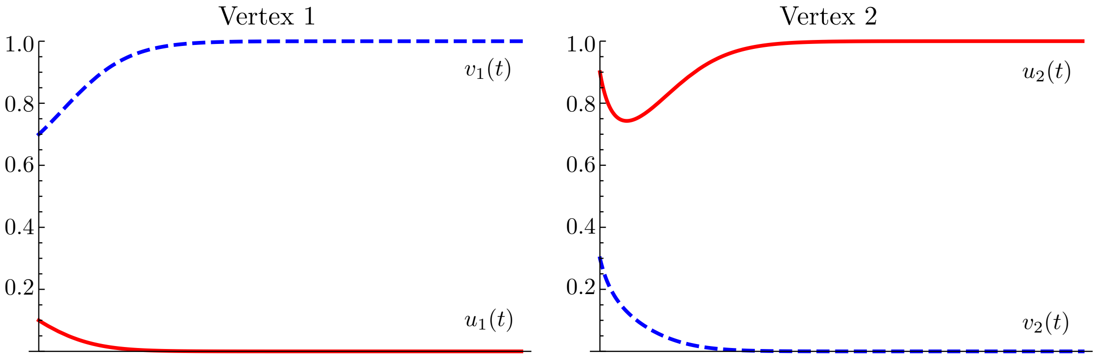

Figure 3: Numerical solution of the Lotka-Volterra model (3.1) on a graph with 2 vertices and 1 edge. Diffusion coefficients are $d_1 = d_2 = 0$.

If d is small and positive, Theorem 5.6 predicts the existence of stable heterogeneous stationary states with positive components close to $(E_1, E_2) = (1, 0, 0, 1)$ and $(E_2, E_1) = (0, 1, 1, 0)$. For example, if $d = 0.05$, a numerical calculation finds stable equilibrium points approximately at $(u_1, v_1, u_2, v_2) = (0.85, 0.05, 0.05, 0.85)$ and $(u_1, v_1, u_2, v_2) = (0.05, 0.85, 0.85, 0.05)$. Figure 4 shows a numerically calculated solution of (3.1) approaching the latter stationary state. We see that species 2 dominates at vertex 1, while species 1 dominates at vertex 2. However, no species becomes extinct: In each vertex, the tendency of the weaker population to extinction is compensated by diffusion from the other vertex.

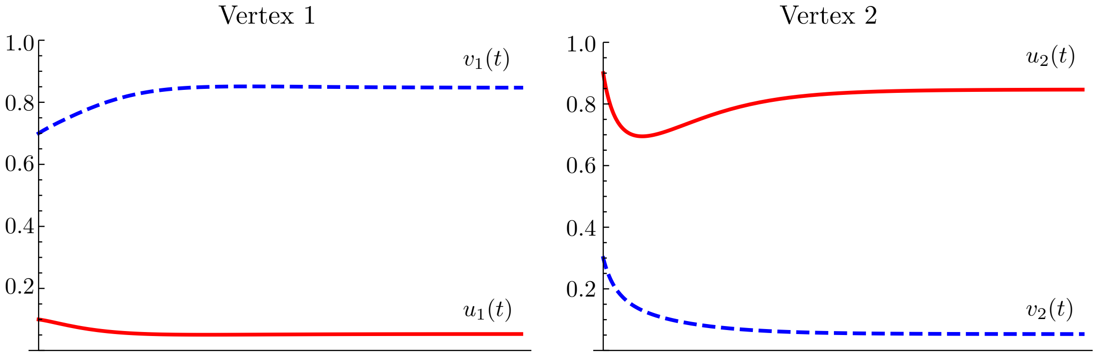

Figure 4: Numerical solution of the same Lotka-Volterra model as in Figure 3, but with diffusion coefficients increased to $d_1 = d_2 = 0.05$.

If we increase the diffusion to $d = 0.2$, numerical calculation finds no heterogeneous stationary states with nonnegative components. Figure 5 shows the solution with the same initial conditions as before. The solution now approaches the homogeneous stationary state $\boldsymbol{E}_2 = (0, 1, 0, 1)$, in which species 2 wins the competition at both vertices, and species 1 is driven to extinction.

Remark 5.8. In the situation of Example 5.7, the two-patch competition model clearly has 16 stationary states for $d = 0$. Page 217 in Levin (1974) says that small coupling destroys 10 of these equilibria, the remaining 6 being the 4 homogeneous stationary states, as well as the 2 heterogeneous states close to

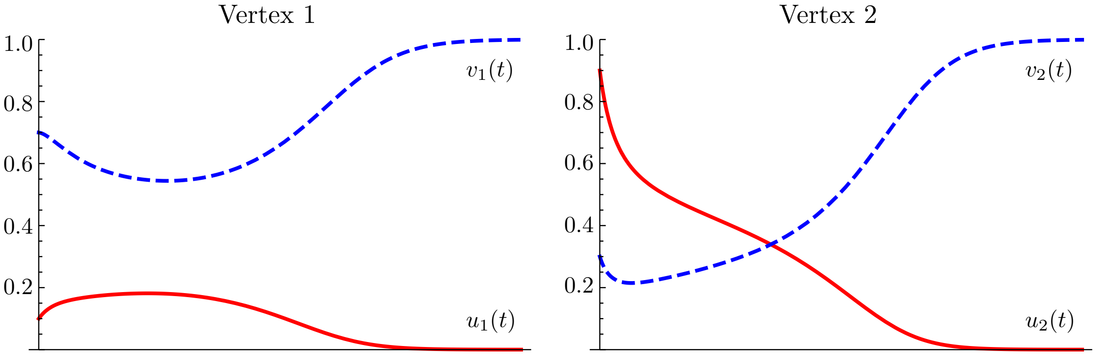

Figure 5: Numerical solution of the same Lotka-Volterra model as in Figure 4, but with diffusion coefficients increased to $d_1 = d_2 = 0.2$.

(E_1, E_2) and (E_2, E_1). Theorem 5.6 shows this claim to be false: In fact, only those equilibria with exactly one component close to E_0 are destroyed (i.e., moved out of the nonnegative orthant); there are 6 of them, while the remaining 10 equilibria remain nonnegative. This fact is easily confirmed by numerical calculation.

6 Concluding remarks and open problems

The biological interpretation of the main results obtained in this paper is as follows:

- $0 < \alpha < 1$, $\beta > 1$: For arbitrary positive initial conditions, species 1 wins the competition in all patches, and species 2 becomes extinct in all patches (see the first part of Theorem 4.5).
- $\alpha > 1$, $0 < \beta < 1$: For arbitrary positive initial conditions, species 2 wins the competition in all patches, and species 1 becomes extinct in all patches (see the second part of Theorem 4.5).
- $0 < \alpha < 1$, $0 < \beta < 1$: For arbitrary positive initial conditions, the populations in each vertex approach the same coexistence state $\left(\frac{1-\alpha}{1-\alpha\beta}, \frac{1-\beta}{1-\alpha\beta}\right)$ (see the third part of Theorem 4.5).
- $\alpha > 1$, $\beta > 1$, large d_1 and d_2: All patches become synchronized – they share the same asymptotic behavior. Depending on the initial conditions, species 1 becomes extinct everywhere, species 2 becomes extinct everywhere, or both species coexist everywhere (see Theorem 5.3). The first two cases are locally stable, the third is unstable (see Theorem 4.2).
- $\alpha > 1$, $\beta > 1$, small d_1 and d_2: The asymptotic behavior depends on the initial conditions, and might be different in different patches – there is no synchronization. For each subset of the n patches, there is a locally stable stationary state such that species 1 dominates in the selected patches (but species 2 still survives there), while species 2 dominates in the remaining patches (but species 1 still survives there). Thus, there exist 2^n locally stable stationary states, and $2^n - 2$ of them are spatially heterogeneous (see Theorem 5.6 and Lemma 5.4).

Finally, we mention the following possible extensions of the results obtained in this paper, as well as topics for further research:

- *Edge-specific diffusion coefficients.* In a more realistic model of Lotka-Volterra type, the diffusion coefficients d_1 and d_2 could be replaced by diffusion matrices $\{d^1_{ij}\}_{i,j=1}^n$ and $\{d^2_{ij}\}_{i,j=1}^n$, where $d^k_{ij} =$

$d^k_{ji} \geq 0$ whenever $i \neq j$. The generalized model has the form

$$\begin{aligned} u_i'(t) &= \sum_{j\neq i} d^1_{ij}(u_j(t) - u_i(t)) + \rho_1 u_i(t)(1 - u_i(t) - \alpha v_i(t)), \qquad i \in V, \\ v_i'(t) &= \sum_{j\neq i} d^2_{ij}(v_j(t) - v_i(t)) + \rho_2 v_i(t)(1 - v_i(t) - \beta u_i(t)), \qquad i \in V. \end{aligned} \tag{6.1}$$

The number d^k_{ij} is the diffusion coefficient between patches i and j for the k-th species; in particular, $d^k_{ij} = 0$ means that the k-th species is unable to move between vertices i and j. The model reflects the fact that the species might prefer certain routes over others.

If we let $L_k = \{l^k_{ij}\}^n_{i,j=1}$, where $l^k_{ij} = -d^k_{ij}$ for $i \neq j$ and $l^k_{ii} = \sum_{j\neq i} l^k_{ij}$, then the previous system can be written in the vector form

$$\begin{aligned} u'(t) &= -L_1 u(t) + \rho_1 f_1(u(t), v(t)), \\ v'(t) &= -L_2 v(t) + \rho_2 f_2(u(t), v(t)). \end{aligned} \tag{6.2}$$

L_1 and L_2 might be interpreted as weighted Laplacian matrices. For example, they are still symmetric, positive semidefinite, and have $(1, \ldots, 1)$ as an eigenvector corresponding to the zero eigenvalue.

Some results obtained in this paper, namely Theorem 3.2, Theorem 3.3, Corollary 3.4, Lemma 4.1 and Theorem 4.2, are still valid in the more general setting. Theorem 5.3 and its proof can be also adapted: The condition that $\min(d_1, d_2)$ is sufficiently large has to be replaced by the requirement that the second smallest eigenvalues of L^1 and L^2 are sufficiently large. Alternatively, one might consider the diffusion coefficients as fixed, and study how the existence of heterogeneous stationary states depends on the growth rates ρ_1 and ρ_2; this approach is also applicable to Theorem 5.6. On the other hand, it is unclear how to generalize Lemma 4.3 and Theorem 4.5. We remark that some information on more general Lotka-Volterra systems with edge-specific diffusion coefficients can be found in Section 5.3 of Takeuchi (1996).

- *Different graphs for different species.* Throughout this paper, we were assuming that both species can move along the edges of the same connected graph G. In a more general model, we might consider two different connected graphs G_1, G_2, one for each species. For example, one species may be able to cross a longer distance between two islands than that crossed by the other species. The corresponding model has the form

$$\begin{aligned} u'(t) &= -d_1 L_1 u(t) + \rho_1 f_1(u(t), v(t)), \\ v'(t) &= -d_2 L_2 v(t) + \rho_2 f_2(u(t), v(t)), \end{aligned} \tag{6.3}$$

  where L_k is the Laplacian matrix of G_k. It is a special case of the model described in the previous paragraph, but is much easier to analyze. In particular, Lemma 4.3 and Theorem 4.5 carry over to the two-graph model without any difficulties, and Theorem 5.6 needs only minor modifications. Therefore, as far as we are aware, all results obtained in this paper are (after a proper modification) still valid for the model with two connected graphs. On the other hand, it might be interesting to investigate what happens for two disconnected graphs, whose connected components do not coincide.

- *Vertex-specific carrying capacities and growth rates.* Our model assumes that each vertex has the same carrying capacity (normalized to be 1), and the growth rates are always ρ_1, ρ_2. In a more general model, the vertices of G might correspond to habitats of different quality, and therefore the growth rates as well as carrying capacities might vary among the vertices. Unfortunately, such model seems very difficult to analyze in full generality. For example, because of different carrying capacities, the concept of homogeneous stationary states no longer makes sense. As far as this paper is concerned, it seems that only Theorems 3.2 and 3.3 carry over (after a proper modification) to the more general setting. Various Lotka-Volterra models on graphs with two or three vertices and vertex-specific carrying capacities as well as growth rates are analyzed e.g. in Ruiz-Herrera and Torres (2018) or Takeuchi (1989).

- *Dependence on the structure of the graph.* In the case when both species are strong competitors ($\alpha, \beta > 1$), Theorem 5.3 shows that strong diffusion leads to synchronization among the vertices. Inspecting the proof of Theorem 5.3, we see that a sufficient condition for the synchronization is

$$\min(d_1, d_2) > \frac{5M}{\lambda_2}, \tag{6.4}$$

where $M = \sup_{(x,y)\in[0,1]^2} \|J(x,y)\|$ and λ_2 is the second smallest eigenvalue of the Laplacian matrix of G. Note that λ_2 is referred to as the algebraic connectivity of G, and its role in synchronizability of networks is well known: Networks with higher connectivity are easier to synchronize. For example, conditions similar to (6.4) appear in the literature dealing with models of mutually coupled oscillators, such as the Kuramoto model in networks; see e.g. Pereira et al. (2014).

  Condition (6.4) is sufficient, but numerical calculations indicate that it is not optimal. Thus, it remains an open problem to find a better sufficient (and perhaps necessary) condition for synchronization in the Lotka-Volterra competition model. Similarly, in Theorem 5.6, it would be interesting to know how the upper bound Δ guaranteeing that the stationary state $F_\sigma(d\delta_1, d\delta_2)$ has nonnegative components for all $d \in [0, \Delta]$ depends on the choice of δ_1, δ_2, as well as the graph G.

- *Other models of population dynamics.* Besides the Lotka-Volterra model, it makes sense to consider other competition, cooperation or predator-prey models from classical population dynamics, and study them in the setting of metapopulations or metacommunities on general graphs. Some methods presented in this paper are not restricted to the Lotka-Volterra model. For example, the construction of Lyapunov functions from Lemma 4.3, or the methods used to show the nonexistence/existence of heterogeneous stationary states for large/small diffusion from Theorems 5.3 and 5.6 are also applicable to other population models.

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