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# Source-sink dynamics on networks: Persistence and extinction

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ABSTRACT

Dynamics of populations with logistic growth leads to global persistence on arbitrary networks, whereas bistable dynamics is always associated with local extinction. In this paper we study a reaction-diffusion model on networks with a combination of both logistic and bistable reactions. We analyze a system of source-sink dynamics on networks with migration survival probabilities and derive conditions for strong persistence or local extinction. We show how the persistence or extinction of small populations depend on the diffusion strength, migration survival probability, network structure, and the sum and distribution of per capita growth rates.



## 1. Introduction

In this paper we establish conditions for persistence and extinction of populations in networks of habitats separated by inhabitable areas. We represent the network of habitats by a connected undirected graph $\mathcal{G} = (V, E)$ with $V$ being a set of vertices (patches) and $E$ denoting a set of undirected edges. We study a reaction-diffusion dynamical system

$$u_i'(t) = d \sum_{j \in \mathcal{N}(i)} (p \cdot u_j(t) - u_i(t)) + u_i(t) g_i(u_i(t)), \quad i \in V,\ t > 0, \tag{1.1}$$

describing the evolution of population $u_i(t)$ at vertex $i \in V$ and its migration among $i$ and its neighbors $j \in \mathcal{N}(i)$. We denote by $d > 0$ a diffusion parameter, $p \in [0, 1]$ a migration survival probability during the transition between the vertices $(i, j) \in E$, $g_i$ a $C^1$ smooth per capita growth rate function at vertex $i \in V$, and $f_i(u_i) = u_i g_i(u_i)$ the reaction function.

Eq. (1.1) has been extensively studied in the safe migration case $p = 1$ and either $g_i(0) > 0$ for all $i \in V$ (unstable origin and persistence) or $g_i(0) < 0$ for all $i \in V$ (asymptotically stable origin and local

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extinction). The former case typically occurs with the logistic population growth and the latter with the bistable one which is typically connected to the strong Allee effect. Sufficient conditions are in both cases independent of the network properties.

In this paper we focus on scenarios in which values $g_i(0)$ do not have the same signs and/or the migration survival probability satisfies $p < 1$. In other words, we allow the combinations of logistic and bistable (and other) local dynamics throughout the network and/or take into account the fact that there is a migration risk in changing habitats. We establish sufficient conditions for the local population extinction and persistence and we are specifically interested in the interaction between the diffusion parameter $d$, per capita growth rates $g_i$, and structural properties of the network $\mathcal{G}$.

*Reaction-diffusion equations and discrete-space media.* Continuous reaction-diffusion equation

$$u_t(x,t) = du_{xx}(x,t) + f(u(x,t)), \quad x \in \mathbb{R},\ t > 0, \tag{1.2}$$

is a fundamental model occurring in many natural applications and serving as the simplest example for various dynamical phenomena, e.g., existence of traveling waves, [12]. Finite spatial discretization of (1.2) leads to the lattice reaction-diffusion equation

$$u_i'(t) = d\sum_{i\in\mathbb{Z}} (u_{i-1}(t) - 2u_i(t) + u_{i+1}(t)) + f(u_i(t)), \quad i \in \mathbb{Z},\ t > 0, \tag{1.3}$$

which exhibits strikingly different behavior, e.g., in the case of bistable nonlinearity $f$ – the existence of large number of heterogeneous stationary solutions [10] and the pinning of traveling waves [15].

The lattice equation (1.3) arises directly in many applications in which the discrete space occurs naturally. More generally, we can consider a graph $\mathcal{G}$ to capture more complex spatial dependencies and we usually limit ourselves to the finite number of vertices $|V| < \infty$. A perfect example are the naturally discrete habitats in population dynamics, which have been extensively studied in the theory of metapopulations [8]. The (often dangerous) fragmentation of species habitats represents an important issue with essential emphasis on the structure of the underlying habitat networks [4]. Specific examples include, e.g., populations of birds on islands separated by water [1], butterflies migrating among unconnected ponds [17]. Considering a graph $\mathcal{G} = (V, E)$ and assuming that $f_i(u_i) = f(u_i)$ leads to the graph differential equation

$$u_i'(t) = d\sum_{j\in\mathcal{N}(i)} (u_j(t) - u_i(t)) + f(u_i(t)), \quad i \in V,\ t > 0. \tag{1.4}$$

In the case of bistable nonlinearity, there exists an exponential (in $n = |V|$) number of stationary solutions of (1.4), [18,20], and the bifurcation mechanisms describing their rise or disappearance depend heavily on the network structure [21] and are far from being well understood.

*Persistence and extinction.* Persistence of species represents an important question in mathematical ecology in general, e.g., [7,19]. Specifically, there is relatively large literature considering the special case of (1.1) with $p = 1$

$$u_i'(t) = d\sum_{j\in\mathcal{N}(i)} (u_j(t) - u_i(t)) + u_i(t)g_i(u_i(t)), \quad i \in V,\ t > 0, \tag{1.5}$$

with the logistic per capita growth rate $g_i(0) > 0$. Motivated by the critical interval length for the continuous reaction-diffusion system (1.2), the paper [1] considered (1.5) on a path graph $\mathcal{G} = \mathcal{P}_n$ coupled with Dirichlet boundary conditions. Comparison techniques were applied to establish persistence for small $d > 0$ and the critical patch number (length of a path). This result has been later generalized using cooperative system

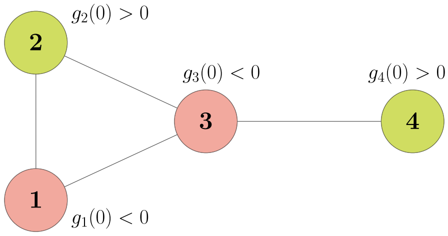



**Fig. 1.** An example of a graph with four vertices – two conditional sinks (vertices 1 and 3) and two conditional sources (vertices 2 and 4). (For interpretation of the colors in the figure, the reader is referred to the web version of this article.)

theory [14]. More importantly, the theory of monotone dynamical systems was used to show that there exists a globally attractive positive equilibrium for any $d > 0$, logistic reaction functions, and any network $\mathcal{G}$, [22].

In the case of a bistable nonlinearity, the origin is trivially asymptotically stable, which corresponds to the local population extinction for small initial populations, [20].

*Source-sink dynamics.* In this paper we focus on the nontrivial related question of combination of patches with $g_i(0) > 0$ and $g_i(0) < 0$, see Fig. 1. Such combination can be naturally implied by various conditions in different habitats (food resources, presence of predators, etc.). Following [13] we call the former conditional sources and the latter conditional sinks. Roughly speaking, once there is no diffusion, small populations are viable in conditional sources whereas they become extinct in conditional sinks. Sources and sinks are a general concept not restricted to mathematical ecology. They occur naturally, e.g., in earth sciences. Consequently, our model can describe also networks of carbon sources and sinks, e.g., regions with coal power plants and forest areas, [13].

*Migration survival probabilities.* Our system (1.1) also incorporates migration survival probability $p \in [0, 1]$ which describes the fact that populations migrating from one location do not necessarily survive the journey. Motivated by migration of Burwash caribou herds and the nonzero migration death probabilities (due to predation of wolves and bears), Freedman et al. [5] studied a model

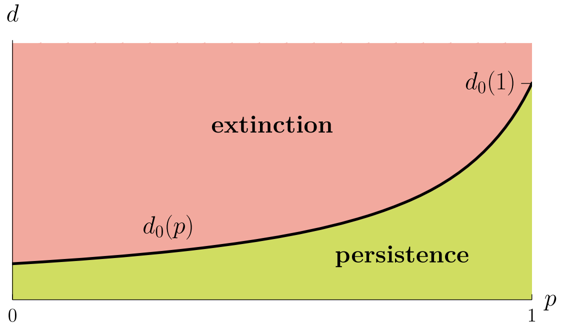
$$u_i'(t) = u_i(t)g_i(u_i(t)) - \varepsilon_i h_i(u_i(t)) + \sum_{j\in\mathcal{N}(i)} \varepsilon_j p_{ji} h_j(u_j(t)), \quad i \in V,\ t > 0, \tag{1.6}$$

where $g_i$ describes a per capita logistic growth rate, i.e., $g_i(0) > 0$, $p_{ji}$ probabilities of successful migration from $j$-th to $i$-th habitat, $\varepsilon_i > 0$ inverse barrier strength in going out of $i$-th vertex and $h_i(u_i)$ is a nonlinear dispersal rate. Given the logistic growth, the paper proves the existence of globally attractive positive equilibrium if $p = 1$ and establishes necessary and sufficient conditions for the existence of positive equilibrium in the case of two habitats, i.e., $n = |V| = 2$.

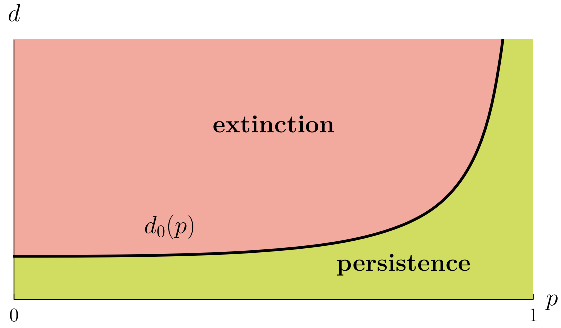
In a closely related model, Chen et al. [3] recently studied a model with asymmetric diffusion

$$u_i'(t) = u_i(t)f_i\left(u_i(t)\right) + \rho \sum_{j=1}^{n} \left(a_{ij}u_j(t) - a_{ji}u_i(t)\right) - \rho\epsilon_i u_i(t), \quad i = 1, \ldots, n, \tag{1.7}$$

where $a_{ij} \geq 0$ is the dispersal capacity along the edge $(j, i) \in E$, $\rho > 0$ represents the dispersal rate, and $\epsilon_i > 0$ is the death rate. The results obtained by Karlin's theorem are in the same direction as ours. We focus more on the dependence of the behavior on migration survival probability $p$ and the network structure in (1.1). In Section 7 we generalize our results for (1.1) to the model with asymmetric dispersal and non-constant $p$.




(a) Sink dominance $\sum_{i\in V} g_i(0) < 0$




(b) Source dominance $\sum_{i\in V} g_i(0) \geq 0$

**Fig. 2.** Strictly increasing threshold function $d_0(p)$ from Theorem 1.1 and two scenarios. If the overall growth rate $\sum_{i\in V} g_i(0)$ is negative there is a threshold value $d_0(1)$ for $p = 1$, if it is positive the population persist for $p = 1$ and all $d > 0$. (For interpretation of the colors in the figure(s), the reader is referred to the web version of this article.)

*Our results.* The system (1.1) is called *uniformly (strongly) persistent* [19, Def. 3.1] if there exists $\varepsilon > 0$ such that every solution $u(t)$ of (1.1) with a nonnegative initial condition $u(0) \neq 0$ satisfies $u_i(t) > 0$ for all $t > 0$ and $i \in V$ and

$$\liminf_{t\to\infty} \|u(t)\| > \varepsilon. \tag{1.8}$$

By *local extinction* we mean a situation in which there exists $\delta > 0$ such that for all initial conditions with $\|u(0)\| < \delta$ we have

$$\lim_{t\to\infty} u(t) = 0.$$

While extinction is directly connected to the attractivity of the origin, the persistence is in general more strict than the concept of instability.

Throughout the paper we assume that there exists at least one conditional source in the network:

(S) There exists $i \in V$ such that $g_i(0) > 0$.

Our main result is the following statement which provides conditions on the diffusion $d$, migration survival probability $p$, and the sign of the overall growth rate $\sum_{i\in V} g_i(0)$ that ensure either persistence or local extinction of populations.

**Theorem 1.1.** *Consider the system (1.1) and assume that (S) is satisfied.*

1. *There exists a strictly increasing and continuous function $d_0(p)$, $d_0 : (0, 1) \to \mathbb{R}^+$, such that for a given $p \in (0, 1)$:*
   (i) *the system (1.1) is uniformly persistent provided $d \in (0, d_0(p))$,*
   (ii) *there is the local extinction in the system (1.1) provided $d > d_0(p)$.*
2. *If $\sum_{i\in V} g_i(0) < 0$, then there exists a finite $d_0(1) = \lim_{p\to 1^-} d_0(p)$ such that for $p = 1$:*
   (i) *the system (1.1) is uniformly persistent provided $d \in (0, d_0(1))$,*
   (ii) *there is the local extinction in the system (1.1) provided $d > d_0(1)$.*
3. *If $\sum_{i\in V} g_i(0) \geq 0$, then $\lim_{p\to 1^-} d_0(p) = \infty$ and the system (1.1) is uniformly persistent for $p = 1$ and every $d \in (0, \infty)$.*

In other words, if $d$ is small the populations persist. Once $d$ crosses the threshold $d_0(p)$ the origin becomes locally asymptotically stable and small populations go extinct. Besides the migration survival probability $p$, the threshold $d_0(p)$ depends on the value of the overall growth rate $\sum_{i\in V} g_i(0)$ and the structural properties of the network $\mathcal{G}$.

The sum $\sum_{i\in V} g_i(0)$ influences not only values $d_0(p)$ qualitatively but also the quantitative behavior in the case without the migration mortality, i.e., $p = 1$. If $\sum_{i\in V} g_i(0) < 0$ the threshold $d_0(1)$ remains for $p = 1$ whereas if $\sum_{i\in V} g_i(0) \geq 0$ there is no threshold and the population persists for all $d > 0$, see Fig. 2.

The main contribution of this paper consists in the description of the properties of the threshold value $d_0(p)$ and its dependence on $p$ and the network structure. In a simple case of $\mathcal{G} = K_2$ we compute $d_0(p)$ explicitly, Section 5. For a general $\mathcal{G}$ we get rough estimates and study it numerically, Section 6.

*Paper structure.* In Section 2 we introduce necessary concepts from algebraic graph theory and prove few auxiliary lemmas. In Section 3 we investigate in detail the situation when migration survival probability satisfies $p \in (0, 1)$. In Section 4 we conclude the proof of Theorem 1.1 by describing the situation for safe migrations with $p = 1$. Next, we show in Section 5 that in the simplest case with two patches, the threshold $d_0(p)$ from Theorem 1.1 can be computed explicitly, which enables us a detailed discussion. In Section 6 we provide estimates on the threshold $d_0(p)$, numerical illustrations of the interplay among the network structure, the diffusion parameter $d$, and the migration survival probability $p$. In Section 7 we generalize our results to the asymmetric dispersal case in the spirit of (1.7) from [3].

## 2. Algebraic reformulation, preliminaries

In this section we use the results from the algebraic graph theory to show that persistence and local extinction of (1.1) depend only on the sign of the maximal eigenvalue of the linearization at the origin. In other words, a single positive (not necessary all) eigenvalue suffices for the persistence of populations because of the structural properties of the problem.

Let us transform the system (1.1) into a vector form. Let $A$ denote the adjacency matrix of the graph $\mathcal{G} = (V, E)$, $D = \operatorname{diag}_{i\in V}(\deg(i))$ be the diagonal matrix of vertex degrees, and $L = D - A$, i.e.,

$$L = (\ell_{i,j}) \quad \text{in which} \quad \ell_{i,j} = \begin{cases} \deg(i), & i = j, \\ -1, & \{i,j\} \in E, \\ 0, & \{i,j\} \notin E, \end{cases}$$

denote the Laplacian matrix of $\mathcal{G}$, [6, Sec. 12]. Further, let $G : \mathbb{R}^n \to \mathbb{R}^{n\times n}$ ($n = |V|$) be the per-capita growth rates in the diagonal matrix form $G(u) = \operatorname{diag}_{i\in V}(g_i(u_i))$. To enlighten the notation we also denote the diagonal of $G(u)$ by $g(u)$, i.e., $g(u) := (g_i(u_i))_{i\in V}$.

We rewrite the system (1.1) into

$$u_i'(t) = dp \sum_{j\in\mathcal{N}(i)} (u_j(t) - u_i(t)) - d(1-p) \sum_{j\in\mathcal{N}(i)} u_i(t) + u_i(t) g_i(u_i(t)), \quad i \in V,\ t > 0.$$

In this form, the second term directly represents the migration losses. Using the vector notation, we can translate it into a concise form

$$u'(t) = -dpLu(t) - d(1-p)Du(t) + G(u(t))u(t), \quad t > 0, \tag{2.1}$$

in which $u(t) = (u_1(t), u_2(t), \dots, u_n(t))^\top$.

Linearizing the vector field

$$F(u; d, p) = -dpLu - d(1-p)Du + G(u)u \tag{2.2}$$

at $u = 0$, we get the Jacobian matrix

$$F'_u(0; d, p) = -dpL - d(1-p)D + G(0). \tag{2.3}$$

The matrix $F'_u(0; d, p)$ is a diagonal perturbation of the matrix $-dpL$ which is itself negative semidefinite. The graph Laplacian matrix $L$ is positive semidefinite and its eigenvalues satisfy

$$0 = \lambda_1(L) < \lambda_2(L) \leq ... \leq \lambda_n(L)$$

and the eigenvector corresponding to $\lambda_1(L)$ is $v_1(L) = \frac{1}{\sqrt{n}}(1, 1, \dots, 1)^\top = \frac{1}{\sqrt{n}}\mathbf{1}$ provided the graph $\mathcal{G}$ is connected, [6, Sec. 12].

All eigenvalues of a symmetric matrix are real and the eigenvectors can be chosen so that they form an orthonormal basis of $\mathbb{R}^n$. Since we are interested in the definiteness of the Jacobian matrix $F'_u(0; d, p)$ we exploit the Courant-Fischer principle ([11, Cor. 3.3]) which characterizes the maximal eigenvalue $\lambda_{\max}(B)$ of a symmetric matrix $B$ as

$$\lambda_{\max}(B) = \max_{\|v\|=1} v^\top Bv = v_{\max}^\top B v_{\max}$$

in which $v_{\max}$ is a unit eigenvector (an element of $\ker(B - \lambda_{\max}(B)I)$ in general) corresponding to the maximal eigenvalue $\lambda_{\max}(B)$.

The matrix $-F'_u(0, d, p)$ from (2.3) and the negative of the adjacency matrix $-A$ of an undirected graph $\mathcal{G}$ are both examples of symmetric generalized graph Laplacians. A square (in general asymmetric) matrix $B$ is a *generalized graph Laplacian* if its entries satisfy

$$B = (b_{i,j}) \quad \text{in which} \quad b_{i,j} \begin{cases} \leq 0, & i \neq j, \\ \in \mathbb{R}, & i = j. \end{cases}$$

The negative of an irreducible generalized graph Laplacian possesses a simple maximal eigenvalue and the corresponding eigenvector is positive.

**Lemma 2.1** *([6, Lem. 13.9.1]). Let $-B$ be an irreducible generalized graph Laplacian. Then $\lambda_{\max}(B)$ is simple and the corresponding eigenvector $v_{\max}(B)$ can be taken to have all its entries positive.*

The Jacobian matrix $F'_u(0; d, p)$ from (2.3) and the adjacency matrix $A$ are irreducible provided the underlying graph $\mathcal{G}$ is connected. The simplicity of $\lambda_{\max}$ implies that the $(d, p)$-dependent branch of the maximal eigenvalue does not intersect other branches.

**Remark 2.2.** To enlighten the text, we introduce the notation

$$\lambda_{\max}(d, p) := \lambda_{\max}(F'_u(0; d, p)).$$

The function $\lambda_{\max}(d, p) : \mathbb{R}^2 \to \mathbb{R}$ is used exclusively in the context of the Jacobian matrix $F'_u(0; d, p)$. Otherwise, we include the whole matrix in the argument $\lambda_{\max}(\cdot)$.

Naturally, if $\lambda_{\max}(d, p) < 0$ the stationary solution $u \equiv 0$ is locally asymptotically stable and small populations go extinct. If $\lambda_{\max}(d, p) > 0$ the solution $u \equiv 0$ is unstable. The following lemma shows that all populations persist in the sense of (1.8) in this case.

**Lemma 2.3** *(uniform persistence). Let $\lambda_{\max}(d,p) > 0$ for $d > 0$ and $p \in (0,1]$. Then there exists $\varepsilon > 0$ such that every solution $u(t)$ of (1.1) with a nonnegative initial condition $u(0) \neq 0$ satisfies $u_i(t) > 0$ for all $t > 0$ and $i \in V$ and*

$$\liminf_{t\to\infty} \|u(t)\| > \varepsilon.$$

**Proof.** The nonnegative orthant

$$\mathcal{Q}^+ = \{u \in \mathbb{R}^n : \ u_i \geq 0 \text{ for every } i \in V\}$$

is positively invariant with respect to the vector field $F(u;d,p)$ given by (2.2), since $F_i(u;d,p) \geq 0$ provided $u_i = 0$ (on the boundary of $\mathcal{Q}^+$). Moreover, there is $F_i(u;d,p) > 0$ for $u_i = 0$ provided $u_j > 0$ for a neighbor vertex $j \in \mathcal{N}(i)$. Via induction throughout the connected graph $\mathcal{G}$, we get that for a nonnegative initial condition $u(0) \neq 0$ there is $u_i(t) > 0$ for all $t > 0$ and $i \in V$.

By Lemma 2.1, the unit eigenvector $v_{\max}$ of the matrix $F'_u(0;d,p)$ corresponding to a simple $\lambda_{\max}(d,p) > 0$ can be chosen such that $v_{\max,i} > 0$ for every $i \in V$. Let us show that there exists $\delta^* > 0$ such that for all $\delta \in (0,\delta^*)$ and all $u \in \mathcal{Q}^+$ lying on the hyperplane $v_{\max}^\top u = \delta$ the vector field $F(u;d,p)$ satisfies

$$v_{\max}^\top F(u;d,p) > 0. \tag{2.4}$$

Assume by contradiction that there exists a sequence $(u_n) \subset \mathcal{Q}^+$ such that $\|u_n\| \to 0^+$ and

$$v_{\max}^\top F(u_n;d,p) = v_{\max}^\top \left(-dpLu_n - d(1-p)Du_n + G(u_n)u_n\right) \leq 0.$$

Dividing the inequality by $\|u_n\| > 0$ and denoting $w_n = u_n/\|u_n\|$ we obtain

$$v_{\max}^\top \left(-dpLw_n - d(1-p)Dw_n + G(u_n)w_n\right) \leq 0.$$

Since $\|w_n\| = 1$ for all $n \in \mathbb{N}$, there is $w_n \to w^* \in \mathcal{Q}^+$, $\|w^*\| = 1$ (at least for a subsequence). By the continuity and (2.3) we therefore obtain

$$v_{\max}^\top \left(-dpLw^* - d(1-p)Dw^* + G(0)w^*\right) = v_{\max}^\top F'_u(0;d,p)w^* \leq 0.$$

Let $w^* = \alpha v_{\max} + z$ in which $\alpha \in \mathbb{R}$ and $z \in (\operatorname{span}(v_{\max}))^\perp$. Since $(\operatorname{span}(v_{\max}))^\perp$ is the eigenspace corresponding to lower eigenvalues of symmetric matrix $F'_u(0;d,p)$, it is invariant to the application of $F'_u(0;d,p)$, i.e., $F'_u(0;d,p)z \in (\operatorname{span}(v_{\max}))^\perp$ and

$$v_{\max}^\top F'_u(0;d,p)(\alpha v_{\max} + z) = \alpha v_{\max}^\top F'_u(0;d,p)v_{\max} = \alpha\lambda_{\max}(d,p)\|v_{\max}\|^2 = \alpha\lambda_{\max}(d,p) \leq 0.$$

Since $\lambda_{\max}(d,p) > 0$, this implies that $\alpha \leq 0$ which contradicts $w^* \in \mathcal{Q}^+$, $\|w^*\| = 1$. Therefore (2.4) holds and $\mathcal{M}_\delta = \left\{u \in \mathcal{Q}^+ : \ v_{\max}^\top u \geq \delta\right\}$ is positively invariant with respect to the vector field $F(u;d,p)$ for every $\delta \in (0,\delta^*]$.

Consequently, there is $v_{\max}^\top u(t) > \delta^*$ for all $t > 0$ provided $v_{\max}^\top u(0) \geq \delta^*$. Let us consider on the contrary an initial condition such that $v_{\max}^\top u(0) = \delta < \delta^*$. We show that even in this case there is $t_0 > 0$ such that $v_{\max}^\top u(t) > \delta^*$ for all $t > t_0$. Indeed, assume by contradiction that $\delta \leq v_{\max}^\top u(t) \leq \delta^*$ for all $t > 0$. Denoting

$$M = \left\{u \in \mathcal{Q}^+ : \ \delta \leq v_{\max}^\top u \leq \delta^*\right\},$$

the continuity of the vector field $F(u;d,p)$ implies the existence of

$$m = \min_{u \in M} v_{\max}^{\top} F(u; d, p) > 0.$$

Since $u(t) = u(0) + \int_0^t F(u(s); d, p)\mathrm{d}s$, we obtain

$$\delta^* \geq v_{\max}^{\top} u(t) = v_{\max}^{\top} u(0) + \int_0^t v_{\max}^{\top} F(u(s); d, p)\ \mathrm{d}s \geq \delta + mt \to \infty \quad \text{for} \quad t \to \infty,$$

a contradiction.

Hence, for every nonnegative initial condition $u(0) \neq 0$ there exists $t_0 > 0$ such that $v_{\max}^{\top} u(t) > \delta^*$ for all $t > t_0$. Finally, since $v_{\max,i} > 0$ for all $i \in V$, the term

$$\|u\|_v = \sum_{i \in V} v_{\max,i} |u_i|$$

defines a norm on $\mathbb{R}^n$. Equivalence of norms guarantees the existence of $c > 0$ such that $c\|u\|_v \leq \|u\|$ for every $u \in \mathbb{R}^n$. Since $u_i(t) > 0$ for all $t > 0$, there is

$$\|u(t)\| \geq c\|u(t)\|_v = cv_{\max}^{\top} u(t) > c\delta^* \quad \text{for all} \quad t > t_0,$$

i.e., for $\varepsilon = c\delta^*/2$ there is

$$\liminf_{t \to \infty} \|u(t)\| \geq c\delta^* > \varepsilon,$$

which concludes the proof. □

**Remark 2.4.** Note that we do not study the case of $\lambda_{\max}(d, p) = 0$. In this situation the attractivity of the solution $u \equiv 0$ is naturally affected by higher order terms of the vector field $F(u; d, p)$ (2.2) which we do not control.

**Remark 2.5.** Note that Lemma 2.3 is no longer valid for $p = 0$. The migration is always unsuccessful and the system splits into $n$ separated independent equations. Such system is persistent if and only if $g_i(0) \geq d \deg(i)$ for all $i \in V$.

Consequently, we analyze the sign of $\lambda_{\max}(d, p)$ of the parameter-dependent matrix $F'_u(0; d, p)$ in the following paragraphs. The following lemma sums up important properties of the spectrum of a general parametric family of symmetric matrices $\alpha \mapsto B(\alpha)$ (see, e.g., [9, Ch. 2]).

**Lemma 2.6.** *Let $\alpha \mapsto B(\alpha)$ be such that the entries of the symmetric matrix $B(\alpha) \in \mathbb{R}^{n \times n}$, $n \in \mathbb{N}$, depend analytically on $\alpha \in \mathbb{R}^m$, $m \in \mathbb{N}$. Then:*

- (P1) *there exist $n$ continuous functions $\alpha \mapsto \lambda_i(\alpha)$ such that $(\lambda_i(\alpha))_{i=1}^n$ is the spectrum of $B(\alpha)$ for each $\alpha \in \mathbb{R}^m$,*
- (P2) *there exists an orthonormal basis $(v_i(\alpha))_{i=1}^n$ continuously dependent on $\alpha \in \mathbb{R}$ such that $B(\alpha)v_i(\alpha) = \lambda_i(\alpha)v_i(\alpha)$ for all $\alpha \in \mathbb{R}^m$.*

*Moreover, if $m = 1$ then the dependence in both cases is analytic.*

The matrix $F'_u(0; d, p)$ is linear in each of its parameters $d$ and $p$. We explore further properties of a parameter-dependent matrix with linear dependence. Namely, perturbation by a positive semidefinite matrix does not lower the maximal eigenvalue.

**Lemma 2.7.** *Let $\alpha \in \mathbb{R}$, let $B, C$ be symmetric matrices, and let $C$ be positive semidefinite. Then $\alpha \mapsto \lambda_{\max}(B + \alpha C)$ is an increasing function. Moreover, it is strictly increasing provided $C$ is either positive definite or*

$$\ker(B - \lambda_{\max}(B)I) \cap \ker C = \{0\}. \tag{2.5}$$

**Proof.** We first show that the function is increasing at $\alpha^* = 0$. Let $\Delta\alpha > 0$ and denote $v_{\max} \neq 0$ the unit eigenvector corresponding to the maximal eigenvalue of the matrix $B$. Then

$$\lambda_{\max}(B + \Delta\alpha\, C) = \max_{\|v\|=1} v^\top (B + \Delta\alpha\, C)v \geq v_{\max}^\top B v_{\max} + \Delta\alpha\, v_{\max}^\top C v_{\max} \geq \lambda_{\max}(B). \tag{2.6}$$

The last inequality is the consequence of the positive semidefiniteness of the matrix $C$ and of $\Delta\alpha > 0$. Naturally, if $C$ is positive definite, then the last inequality is strict.

Assume now by contradiction that $\lambda_{\max}(B + \Delta\alpha\, C) = \lambda_{\max}(B)$. Then there are equalities in (2.6) and thus

$$(B + \Delta\alpha\, C)v_{\max} = \lambda_{\max}(B + \Delta\alpha\, C)v_{\max} \qquad \text{and} \qquad Cv_{\max} = 0$$

by the Courant-Fischer principle. These identities yield

$$Bv_{\max} = \lambda_{\max}(B + \Delta\alpha C)v_{\max} = \lambda_{\max}(B)v_{\max}.$$

Then surely $v_{\max} \in \ker(B - \lambda_{\max}(B)I) \cap \ker C$, a contradiction with (2.5).

Now, set $\alpha^* \in \mathbb{R}$. Then the function $\Delta\alpha \mapsto \lambda_{\max}(B + \alpha^* C + \Delta\alpha\, C)$ is increasing. It is strictly increasing if either $C$ is positive definite or

$$\ker(B + \alpha^* C - \lambda_{\max}(B + \alpha^* C)I) \cap \ker(C) = \{0\}.$$

Assume that there exists $v := v(\alpha^*)$ such that $\|v(\alpha^*)\| = 1$ and

$$v(\alpha^*) \in \ker(B + \alpha^* C - \lambda_{\max}(B + \alpha^* C)I) \cap \ker(C).$$

Then

$$(B + \alpha^*\, C)v(\alpha^*) = \lambda_{\max}(B + \alpha^*\, C)v(\alpha^*) \qquad \text{and} \qquad Cv(\alpha^*) = 0$$

and subsequently

$$Bv(\alpha^*) = (B + \alpha^* C)v(\alpha^*) = \lambda_{\max}(B + \alpha^* C)v(\alpha^*).$$

Thus $\lambda_{\max}(B + \alpha^* C)$ is an eigenvalue of $B$ for any $\alpha^* \in \mathbb{R}$. Since the function $\alpha^* \mapsto \lambda_{\max}(B + \alpha^* C)$ is continuous (Lemma 2.6), the image of the set $\mathbb{R}$ must be a connected set. The spectrum of a matrix $B$ is a finite union of points and thus $\alpha^* \mapsto \lambda_{\max}(B + \alpha^* C)$ must be a constant function. Moreover, $\lambda_{\max}(B + \alpha^* C) = \lambda_{\max}(B)$ for $\alpha^* = 0$ and we can add the final equality

$$Bv(\alpha^*) = (B + \alpha^* C)v(\alpha^*) = \lambda_{\max}(B + \alpha^* C)v(\alpha^*) = \lambda_{\max}(B)v(\alpha^*).$$

Thus, $v(\alpha^*) \in \ker(B - \lambda_{\max}(B)I) \cap \ker(C)$, a contradiction with (2.5). $\square$

**Corollary 2.8.** *Let $\alpha \in \mathbb{R}$, let $B, C$ be symmetric matrices, and let $C$ be negative semidefinite. Then $\alpha \mapsto \lambda_{\max}(B + \alpha C)$ is a decreasing function. Moreover, it is strictly decreasing provided $C$ is either negative definite or*

$$\ker(B - \lambda_{\max}(B)I) \cap \ker C = \{0\}.$$

Moreover, the maximal eigenvalue exhibits a convex dependence on the parameter $\alpha \in \mathbb{R}$.

**Lemma 2.9.** *Let $\alpha \in \mathbb{R}$ and let $B, C$ be symmetric matrices. Then $\alpha \mapsto \lambda_{\max}(B + \alpha C)$ is a convex function.*

**Proof.** By a straightforward application of the Courant-Fischer principle we have

$$\lambda_{\max}(B_1 + B_2) \le \lambda_{\max}(B_1) + \lambda_{\max}(B_2)$$

for any pair of symmetric matrices $B_1, B_2$.

Set $\alpha := t\alpha_1 + (1-t)\alpha_2$ for $t \in (0,1)$ and $\alpha_1 < \alpha_2$. Then

$$\begin{aligned}\lambda_{\max}(B + \alpha C) &= \lambda_{\max}(tB + t\alpha_1 C + (1-t)B + (1-t)\alpha_2 C)\\ &\le t\lambda_{\max}(B + \alpha_1 C) + (1-t)\lambda_{\max}(B + \alpha_2 C). \quad \square\end{aligned}$$

Thanks to Lemmas 2.1 and 2.6, we can formulate stronger regularity statements for $\lambda_{\max}(d,p)$ and describe its monotonicity in particular parameters $d$ and $p$.

**Corollary 2.10.** *The functions $\lambda_{\max}(\,\cdot\,, p) : \mathbb{R}^+ \to \mathbb{R}$ for $p \in [0,1]$ and $\lambda_{\max}(d,\,\cdot\,) : (0,1) \to \mathbb{R}$ for $d \ge 0$ are analytic. Moreover, the function $\lambda_{\max}(\,\cdot\,,\,\cdot\,) : \mathbb{R}_0^+ \times [0,1] \to \mathbb{R}$ is continuous.*

**Proof.** The continuity of $\lambda_{\max}$ is an immediate consequence of Lemma 2.6.

Lemma 2.1 ensures the analyticity of the function $\lambda_{\max}(\,\cdot\,, p) : \mathbb{R}^+ \to \mathbb{R}$ for $p \in (0,1]$ since $F_u'(0; d, p)$ is irreducible. If $p = 0$ then $F_u'(0; d, 0) = -dD + G(0)$ is a diagonal matrix whose eigenvalues scale linearly in $d$ and is thus analytic too.

In a similar manner, Lemma 2.1 ensures the analyticity of the function $\lambda_{\max}(d,\,\cdot\,) : (0,1) \to \mathbb{R}$ for $d > 0$. The case $d = 0$ again breaks the irreducibility assumption. Nevertheless $F_u'(0; 0, p) = G(0)$ is a constant matrix and its eigenvalues are thus trivially analytic in $p$. $\square$

**Corollary 2.11.**

(i) *The function $\lambda_{\max}(\,\cdot\,, p) : \mathbb{R}_0^+ \to \mathbb{R}$ is strictly decreasing for every fixed $p \in [0,1)$. It is moreover strictly decreasing for $p = 1$ provided there exist $i, j \in V$, $i \ne j$ such that $g_i(0) \ne g_j(0)$.*

(ii) *The function $\lambda_{\max}(d,\,\cdot\,) : (0,1) \to \mathbb{R}$ is strictly increasing for every fixed $d > 0$.*

**Proof.** (i) Let $p \in [0,1]$ be fixed and let $d = d^* + \Delta d > 0$ such that $d^* \ge 0$ and $\Delta d > 0$. Then

$$\begin{aligned}F_u'(0; d, p) &= -(d^* + \Delta d)pL - (d^* + \Delta d)(1-p)D + G(0)\\ &= -d^*pL - d^*(1-p)D + G(0) - \Delta d\,(pL + (1-p)D)\\ &= F_u'(0; d^*, p) - \Delta d\,(pL + (1-p)D).\end{aligned}$$

If $p \in [0,1)$ then $pL + (1-p)D$ is a positive definite matrix. Indeed, $L$ is positive semidefinite and $D$ is positive definite since the graph $\mathcal{G}$ is connected and vertex degrees satisfy $\deg(i) > 0$, $i \in V$. Therefore, $d \mapsto \lambda_{\max}(d,p)$ is strictly decreasing by Lemma 2.7. Let $p = 1$, then we have

$$F_u'(0; d, 1) = -dL + G(0).$$

The kernel of the graph Laplacian is generated by a single vector $v_{\max}(-L) = \frac{1}{\sqrt{n}}\mathbf{1}$. If there exist $i, j \in V$ such that $g_i(0) \neq g_j(0)$ then $v_{\max}(L) = \frac{1}{\sqrt{n}}\mathbf{1} \notin \ker(G(0) - \lambda_{\max}(G(0))I)$. The function $d \mapsto \lambda_{\max}(d, 1)$ is then strictly decreasing by Lemma 2.7.

(ii) Let $d > 0$ be fixed and let $p = p^* + \Delta p$ be such that $p, \Delta p \in (0, 1)$ and $p^* \in (0, 1)$. Then

$$\begin{aligned} F_u'(0; d, p) &= -d(p^* + \Delta p)L - d(1 - (p^* + \Delta p))D + G(0) \\ &= d\,\Delta p\,(-L + D) - dp^*L - d(1 - p^*)D + G(0) \\ &= d\,\Delta p\,A + F_u'(0; d, p^*), \end{aligned}$$

in which $A = D - L$ is the adjacency matrix of the graph. Let $v_{\max}$ be the maximal eigenvector of the matrix $F_u'(0; d, p^*)$. Then $v_{\max}$ can be taken to have only positive entries by Lemma 2.1 and thus

$$\begin{aligned} \lambda_{\max}(d, p) &= \max_{\|v\|=1} v^\top F_u'(0; d, p)v \geq v_{\max}^\top F_u'(0; d, p)v_{\max} \\ &= d\,\Delta p\, v_{\max}^\top A v_{\max} + v_{\max}^\top F_u'(0; d, p^*)v_{\max} = d\,\Delta p\, v_{\max}^\top A v_{\max} + \lambda_{\max}(d, p^*) \\ &> \lambda_{\max}(d, p^*), \end{aligned} \tag{2.7}$$

since the matrix $A$ has nonnegative entries and $\Delta p > 0$. □

**Remark 2.12.** Note that the statement (i) can be alternatively proven by Karlin's theorem, e.g., [2, Thm. 6]. See for example Chen et al. [3] to see such an application for a related model (1.7). Note that the item (ii) is not covered by Karlin's theorem.

Corollary 2.11 provides a key tool for our main results in the forthcoming sections. One can directly compute that for $d = 0$

$$F_u'(0; 0, p) = G(0) \qquad \text{for all} \qquad p \in [0, 1],$$

and the assumption (S) then ensures that $\lambda_{\max}(0, p) > 0$ for $p \in [0, 1]$. We focus on the question whether the function $d \mapsto \lambda_{\max}(d, p)$ goes to negative values for $d \to \infty$.

## 3. Uncertain migration between patches $p \in [0, 1)$

We start with the examination of the case of uncertain migrations between patches, i.e., $p \in [0, 1)$. Our first result states that weak (possibly positive) per capita growth rates $g_i(0)$ lead to local extinction.

**Lemma 3.1.** *Let*

$$g_i(0) \leq d(1 - p)\deg(i) \quad \text{for every} \quad i \in V \tag{3.1}$$

*and at least one inequality be strict. Then* $\lambda_{\max}(d, p) < 0$.

**Proof.** There is $F_u'(0; d, p) = -dpL - d(1 - p)D + G(0)$. The matrix $-dpL$ is negative semidefinite. Since the diagonal matrix

$$P(0; d, p) = -d(1 - p)D + G(0)$$

is also negative semidefinite thanks to (3.1), the sum $F'_u(0, d, p) = -dpL + P(0; d, p)$ is negative semidefinite as well.

Assume that there exists a nontrivial vector $v \neq 0$ such that

$$v^\top(-dpL + P(0; d, p))v = 0.$$

Then

$$v^\top(-dpL)v = 0 \quad \text{and} \quad v^\top P(0; d, p)v = 0. \tag{3.2}$$

The kernel $\ker(-dpL)$ is generated by the vector $\mathbf{1} = (1, 1, \dots, 1)^\top$ and thus, $v = \alpha\mathbf{1}$, $\alpha \neq 0$. Since $P(0; d, p)$ is a diagonal matrix and due to (3.1) and to the fact that at least one inequality in (3.1) is strict, there is

$$v^\top P(0; d, p)v = \alpha^2 \mathbf{1}^\top P(0; d, p)\mathbf{1} = \alpha^2 \sum_{i \in V} (-d(1-p)\deg(i) + g_i(0)) < 0,$$

a contradiction with (3.2). □

Lemma 3.1 immediately implies that for a fixed migration survival probability $p \in (0, 1)$ the extinction occurs whenever the diffusion $d$ is strong enough. This enables us to define the threshold function $d_0(p)$ (see Fig. 2).

**Corollary 3.2.** *Let $p \in (0, 1)$ be fixed. Then:*

(i) *there is $\lambda_{\max}(d, p) < 0$ for all sufficiently large $d \gg 1$,*
(ii) *there exists a unique $d_0(p)$ such that $\lambda_{\max}(d_0(p), p) = 0$.*

**Proof.** Since (3.1) is satisfied for $p \in (0, 1)$ fixed and $d \gg 1$ sufficiently large, the first statement follows immediately from Lemma 3.1. The second statement is then a consequence of the fact that $\lambda_{\max}(\,\cdot\,, p)$ is continuous (Corollary 2.10) and strictly decreasing (Corollary 2.11). □

The threshold $d_0(p)$ is continuous and strictly increasing in $p$.

**Corollary 3.3.** *The function $p \mapsto d_0(p)$, $p \in (0, 1)$, satisfies:*

(i) *it is continuous,*
(ii) *it is strictly increasing,*
(iii) $\lim_{p \to 0^+} d_0(p) = \max_{i \in V} \frac{g_i(0)}{\deg(i)}$.

**Proof.** The function $d_0(p)$ is correctly defined by Corollary 3.2.

(i) Let us show that $d_0$ is continuous at $p^* \in (0, 1)$. Let $p_n \to p^* \in (0, 1)$. Then, Lemma 3.1 yields that $d_0(p_n)$ is bounded and thus, $d_0(p_n) \to d^* > 0$ (at least for a subsequence). Since $\lambda_{\max}(d_0(p_n), p_n) = 0$, the continuity of the function $\lambda_{\max}(\,\cdot\,,\,\cdot\,)$ (Corollary 2.10) yields that $\lambda_{\max}(d^*, p^*) = 0$. Since $\lambda_{\max}(\,\cdot\,, p^*)$ is strictly decreasing (Corollary 2.11) there has to be $d^* = d_0(p^*)$.
(ii) Let $0 \leq p_1 < p_2 < 1$. Then $0 = \lambda_{\max}(d_0(p_1), p_1) < \lambda_{\max}(d_0(p_1), p_2)$, since $\lambda_{\max}(d_0(p_1),\,\cdot\,)$ is strictly increasing. Thus, $d_0(p_2) > d_0(p_1)$ because $\lambda_{\max}(d_0(p_2), p_2) = 0$ by definition of $d_0(p_2)$ and $\lambda_{\max}(\,\cdot\,, p_2)$ is strictly decreasing. Consequently, $d_0(p)$ is a strictly increasing function.

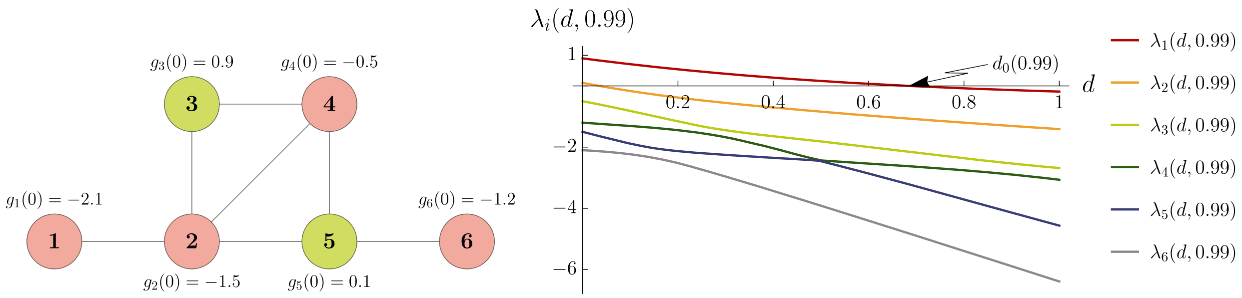



**Fig. 3.** Graph $\mathcal{G}$ with per capita growth rates $g(0)$ from Example 3.4 and the six eigenvalues of $F'_u(0, d, .99)$. (For interpretation of the colors in the figure(s), the reader is referred to the web version of this article.)

(iii) Since $\lambda_{\max}(d, 0) = \max_{i\in V}(-d\deg(i) + g_i(0))$ it is possible to uniquely define $d_0$ in the border value $p = 0$, namely $d_0(0) := \max_{i\in V} \frac{g_i(0)}{\deg(i)}$. Note that the proof of the item (i) can be extended to the interval $p^* \in [0, 1)$ and $d_0$ is thus continuous also at $p = 0$. Therefore,

$$\lim_{p\to 0^+} d_0(p) = d_0(0) = \max_{i\in V} \frac{g_i(0)}{\deg(i)}. \quad \square$$

For the sake of clarity, we end this section with numerical example illustrating various properties of $\lambda_{\max}(d, p)$.

**Example 3.4.** Let us consider a graph $\mathcal{G}$ given in the left panel of Fig. 3. Let the per capita growth rates be given by the vector $g(0) = (-2.1, -1.5, 0.9, -0.5, 0.1, -1.2)^\top$. The migration survival probability is set to $p = 0.99$. We labeled the eigenvalues such that $\lambda_6(d, p) \le \lambda_5(d, p) \le \ldots \le \lambda_{\max}(d, p)$. Lemma 2.6 ensures the existence of six analytic eigenvalue branches which do not necessarily coincide with our notation. Indeed, $\lambda_4(\cdot\,, 0.99)$ and $\lambda_5(\cdot\,, 0.99)$ intersect for $d_1 \doteq 0.5$. By Lemma 2.6 we can switch the labeling $4 \leftrightarrow 5$ at $d_1$ to preserve the analyticity of the branches.

The eigenvalues at $d = 0$ are the entries of the vector $g(0)$ since $F'_u(0; 0, p) = G(0) = \mathrm{diag}_{i\in V}\, g_i(0)$ is a diagonal matrix for any $p \in [0, 1]$. In accordance with Corollary 2.11, the greatest eigenvalue $\lambda_{\max}(d, 0.99)$ is a strictly decreasing and a convex function. Finally, there is $d_0(0.99) \doteq 0.69$ such that $\lambda_{\max}(d_0(0.99), 0.99) = 0$ existence of which is ensured by Corollary 3.2.

## 4. Safe migration $p = 1$ and proof of Theorem 1.1

In this section we consider the case with safe migrations $p = 1$ and show that the existence of the threshold $d_0(1)$ and the eventual population extinction depend on the sign of the sum $\sum_{i\in V} g_i(0)$.

**Theorem 4.1.**

(i) *If $\sum_{i\in V} g_i(0) < 0$, then there exists unique $d_0(1) > 0$ such that*

$$\lambda_{\max}(d_0(1), 1) = 0 \quad \text{and} \quad d_0(1) = \lim_{p\to 1^-} d_0(p).$$

(ii) *If $\sum_{i\in V} g_i(0) \ge 0$, then $\lambda_{\max}(d, 1) > 0$ for every $d > 0$ and $\lim_{p\to 1^-} d_0(p) = \infty$.*

In order to characterize the existence of $d_0(1)$ from Theorem 4.1 we reformulate the problem of determining the definiteness of $F'_u(0; d, p)$. Let us define a matrix function $H$ by

$$F'_u(0; d, 1) = d\left(-L + \tfrac{1}{d}G(0)\right) =: dH\left(\tfrac{1}{d}\right) = dH(\nu), \tag{4.1}$$

in which $\nu = 1/d > 0$, i.e.,

$$H(\nu) := -L + \nu G(0). \tag{4.2}$$

Note that

$$\lambda_i(H(\nu)) = \tfrac{1}{d}\lambda_i(F'_u(0; d, p))$$

for each $i \in V$ and $d = 1/\nu > 0$. This substitution enables us to examine the behavior of $\lambda_{\max}(H(\nu))$ for $\nu \ll 1$ instead of the limit $\lambda_{\max}(F'_u(0; d, 1))$ for $d \gg 1$.

Let us note that in the following analysis it is necessary to consider $\nu \geq 0$ although $H(0)$ does not have a direct correspondence to $F'_u(0; d, p)$. We start with an auxiliary lemma which ensures population persistence for sufficiently strong per capita growth rates $g_i(0)$.

**Lemma 4.2.** *Let $\nu = 1/d$ and let there exist a vertex $i \in V$ such that*

$$\nu g_i(0) > \deg(i).$$

*Then $\lambda_{\max}(H(\nu)) > 0$.*

**Proof.** Let $\delta_{ij}$ be the Kronecker delta (i.e., $\delta_{ij} = 1$ provided $i = j$, otherwise $\delta_{ij} = 0$). Then

$$\lambda_{\max}(H(\nu)) = \max_{\|v\|=1} v^\top H(\nu)v \geq \delta_{i\cdot}^\top H(\nu)\delta_{i\cdot} = -\deg(i) + \nu g_i(0) > 0. \quad \square$$

Note that $\lambda_{\max}(H(0)) = \lambda_{\max}(-L) = 0$ and that (S) together with Lemma 4.2 grant the existence of a threshold value for $\nu$ above which $\lambda_{\max}(H(\nu))$ is always positive. Let us show what happens for $\nu \ll 1$. We first state a characterization theorem for the sign of any eigenvalue of the matrix $H(\nu)$.

**Lemma 4.3.** *Let $(\lambda, v)$ be an eigenpair of $H(\nu)$ for $\nu = 1/d > 0$ such that $\sum_{i\in V} v_i > 0$. Then*

$$\operatorname{sign}(\lambda) = \operatorname{sign}(g(0)^\top v).$$

**Proof.** Since $(\lambda, v)$ is an eigenpair, then

$$\lambda v = H(\nu)v = (-L + \nu G(0))v = -Lv + \nu G(0)v.$$

Next multiply the equation by $\mathbf{1}^\top$ from the left

$$\lambda \sum_{i\in V} v_i = -\mathbf{1}^\top Lv + \nu g(0)^\top v = \nu g(0)^\top v.$$

The positivity of $\nu > 0$ and $\sum_{i\in V} v_i > 0$ conclude the proof. $\square$

In the case of $\sum_{i\in V} g_i(0) < 0$ we can then show the existence of a threshold value $\nu_0$.

**Lemma 4.4.** *Let $g(0)$ be such that $\sum_{i\in V} g_i(0) < 0$. Then there exists $\nu_0 > 0$ such that $\lambda_{\max}(H(\nu)) < 0$ for all $\nu \in (0, \nu_0)$ and $\lambda_{\max}(H(\nu)) > 0$ for $\nu > \nu_0$.*

**Proof.** We know that $\lambda_{\max}(H(\nu))$ is an analytic function by Lemma 2.6 and the fact that it is a generalized graph Laplacian. It is moreover convex by Lemma 2.9.

Surely $\lambda_{\max}(H(0)) = \lambda_{\max}(-L) = 0$ and at the same time, we know that $\lambda_{\max}(H(\nu)) > 0$ for sufficiently large $\nu$ by Lemma 4.2. We show that $\lambda_{\max}(H(\nu)) < 0$ for $0 < \nu \ll 1$.

The simple eigenvector (Lemma 2.1) $v_{\max}(H(\nu))$ is an analytic function of the parameter $\nu \geq 0$ by Lemma 2.6 and also $v_{\max}(H(0)) = \frac{1}{\sqrt{n}}\mathbf{1}^\top$ holds. Thus, there exists $\nu_1 > 0$ such that $\sum_{i\in V} v_{\max,i}(H(\nu)) > 0$ for all $0 < \nu < \nu_1$. From Lemma 4.3 we have that $\operatorname{sign}(\lambda_{\max}(H(\nu))) = \operatorname{sign}(g(0)^\top v_{\max}(H(\nu)))$ for all $\nu > 0$ such that $\sum_{i\in V} v_{\max}(H(\nu)) > 0$. A direct computation yields

$$g(0)^\top v_{\max}(H(0)) = \frac{1}{\sqrt{n}} g(0)^\top \mathbf{1} = \frac{1}{\sqrt{n}} \sum_{i\in V} g_i(0) < 0$$

and again from continuity there exists $\nu_2 > 0$ such that $g(0)^\top v_{\max}(H(\nu)) < 0$ for all $0 \leq \nu < \nu_2$. Therefore, $\lambda_{\max}(H(\nu)) < 0$ for the same choice of $\nu$. The continuity and Lemma 4.2 imply the existence of

$$\nu_0 > \min\{\nu_1, \nu_2\} \qquad \text{such that} \qquad \lambda_{\max}(H(\nu_0)) = 0.$$

The uniqueness of $\nu_0$ results from the convexity of $\lambda_{\max}(H(\nu))$. □

Lemma 4.4 enables us to prove Theorem 4.1.

**Proof of Theorem 4.1.** The first part is a consequence of Lemma 4.4 which yields the existence of some $0 < \nu_0 < \infty$ in which the matrix $H(\,\cdot\,)$ changes its definiteness. Subsequently, there exists $0 < d_0(1) := 1/\nu_0 < \infty$ for which the matrix $F'_u(0;\,\cdot\,,1)$ changes its definiteness.

For the second part of the statement, we use the fact that the inequality

$$\lambda_{\max}(d,1) = \max_{\|v\|=1} v^\top F'_u(0;d,1)v \geq \mathbf{1}^\top F'_u(0;d,1)\mathbf{1} = -d\mathbf{1}^\top L\mathbf{1} + \mathbf{1}^\top G(0)\mathbf{1} = \sum_{i\in V} g_i(0)$$

holds for all $d \geq 0$. If $\sum_{i\in V} g_i(0) > 0$ then $\lambda_{\max}(d,1) > 0$ for all $d \geq 0$.

Assume now that $\sum_{i\in V} g_i(0) = 0$. Then surely $\lambda_{\max}(d,1) \geq 0$ for all $d \geq 0$. Also, the matrix $G(0)$ cannot have a constant diagonal (contradiction with (S)), i.e., there exist $i, j \in V$ such that $g_i(0) \neq g_j(0)$ and thus $\lambda_{\max}(d,1)$ is strictly decreasing by Corollary 2.11. A strictly decreasing and nonnegative function satisfying $\lambda_{\max}(0,1) = \max_{i\in V} g_i(0) > 0$ cannot ever attain its lower bound, i.e., $\lambda_{\max}(d,1) > 0$ for all $d \geq 0$. □

Finally, we can combine Theorem 4.1 and Corollaries 3.2, 3.3 to prove our main result, Theorem 1.1.

**Proof of Theorem 1.1.** Corollary 3.2 ensures existence of $d_0(p)$ such that $\lambda_{\max}(d_0(p),p) = 0$. The function $d_0(p)$ is strictly increasing by Corollary 3.3. Lemma 2.3 together with the fact that $\lambda_{\max}(\,\cdot\,,p)$ is strictly decreasing (Corollary 2.11) and $\lambda_{\max}(0,p) = \max_{i\in V} g_i(0) > 0$ (assumption (S)) implies the persistence in the case $d \in (0, d_0(p))$ in the item 1. The asymptotic stability of the origin in the case $d > d_0(p)$ is then sufficient for the presence of the local extinction in the system (1.1).

The items 2. and 3. are a consequence of Theorem 4.1 and Lemma 2.3. □

## 5. Two patches

In this section we study in detail the simplest case, in which there are only two patches and $\mathcal{G} = K_2$. The system (1.1) can be then rewritten as

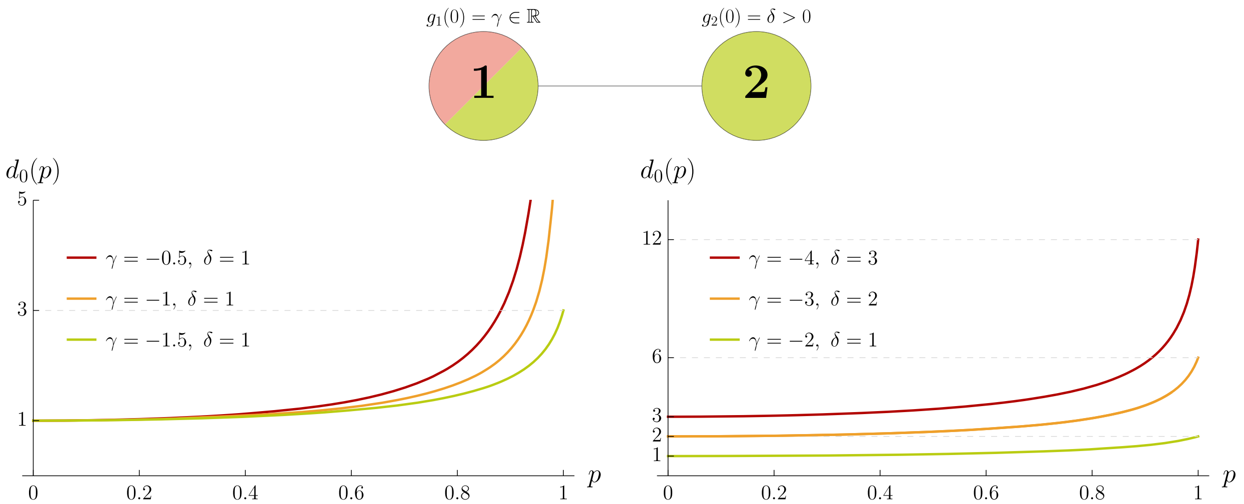



**Fig. 4.** Two patches configuration from § 5 and illustration of Theorem 5.1. The threshold $d_0(p)$ from (5.2) is strictly increasing in $\gamma$ (the left panel) and $\delta$. However, $d_0(p)$ does not depend on $\gamma+\delta$. This sum determines only the existence of a finite threshold $d_0(1)$ (the right panel). (For interpretation of the colors in the figure(s), the reader is referred to the web version of this article.)

$$\begin{cases} u_1'(t) = d\,(p \cdot u_2(t) - u_1(t)) + u_1(t)g_1(u_1(t)), & t > 0, \\ u_2'(t) = d\,(p \cdot u_1(t) - u_2(t)) + u_2(t)g_2(u_2(t)). \end{cases} \tag{5.1}$$

We assume that $g_1(0) = \gamma \in \mathbb{R}$ and $g_2(0) = \delta > 0$ so that (S) is satisfied, see Fig. 4.

Naturally, two patches configurations are the simplest graph (or metapopulation) models and have been extensively studied in the literature (e.g., [5,8,20]). In our case, we are able to get exact threshold $d_0(p)$ and describe its properties.

**Theorem 5.1.** *Let us consider (5.1) with $g_1(0) = \gamma \in \mathbb{R}$ and $g_2(0) = \delta > 0$. Then:*

(a) *the threshold $d_0(p)$ from Theorem 1.1 is*

$$d_0(p) = \frac{\gamma + \delta + \sqrt{(\gamma-\delta)^2 + 4p^2\gamma\delta}}{2(1-p^2)}, \tag{5.2}$$

(b) *$d_0(p)$ is strictly increasing in $\gamma$ and $\delta$,*

(c)

$$\lim_{p \to 1^+} d_0(p) = \begin{cases} \infty & \text{if } \gamma + \delta \geq 0, \\ \frac{\gamma\delta}{\gamma+\delta} & \text{if } \gamma + \delta < 0. \end{cases} \tag{5.3}$$

**Proof.** Linearization of (5.1) at $u \equiv 0$ yields

$$F_u'(0; d, p) = \begin{pmatrix} \gamma - d & dp \\ dp & \delta - d \end{pmatrix}$$

with corresponding eigenvalues

$$\lambda_{1,2} = \frac{\gamma + \delta - 2d \pm \sqrt{(\gamma-\delta)^2 + 4d^2p^2}}{2}.$$

It follows that the larger eigenvalue $\lambda_2$ vanishes once

$$(\gamma + \delta - 2d)^2 = (\gamma - \delta)^2 + 4d^2p^2.$$

Solving the quadratic equation in $d$ we get (5.2).

Next, differentiating (5.2) with respect to $\gamma$ we obtain

$$\frac{\partial d_0(p)}{\partial \gamma} = \frac{\sqrt{(\gamma-\delta)^2 + 4p^2\gamma\delta} + \gamma - \delta + 2p^2\delta}{2(1-p^2)\sqrt{(\gamma-\delta)^2 + 4p^2\gamma\delta}}.$$

The denominator is clearly positive and so is the numerator since

$$(\gamma - \delta)^2 + 4p^2\gamma\delta - (\gamma - \delta + 2p^2\delta)^2 = 4p^2(1-p^2)\delta > 0.$$

Consequently, we have $\frac{\partial d_0(p)}{\partial \gamma} > 0$, the inequality $\frac{\partial d_0(p)}{\partial \delta} > 0$ can be shown in the same fashion.

Finally, as $p \to 1^-$ we get (5.3) by observing that the numerator in (5.2) is always positive if $\gamma + \delta \geq 0$ and by applying the l'Hôspital rule if $\gamma + \delta < 0$. □

**Remark 5.2.** The sum $\sum g_i(0) = \gamma + \delta$ was shown in Theorem 1.1 to play a key role in determining whether the limit $\lim_{p\to 1^-} d_0(p)$ is finite or infinite (and consequently whether the population can become extinct for large diffusion $d \gg 0$ and the case without migration mortality $p = 1$). This is also corroborated by (5.3). However, Eq. (5.2) implies immediately that $\sum g_i(0) = \gamma + \delta$ does not influence the exact value of $d_0(p)$, see Fig. 4.

We illustrate in the following section that, in general, it is a distribution of per capita growth rates $g_i(0)$, and the network structure of $\mathcal{G}$ that determines the exact value of $d_0(p)$.

## 6. Numerical examples and discussion

For general graphs we are unable to compute $d_0(p)$ explicitly as in the previous section. Therefore, we provide numerical illustrations of the behavior of the parameter-dependent matrix $F_u'(0; d, p)$ and the threshold value $d_0(p)$. Theorem 1.1 implies two qualitatively different regimes of the function $d_0(p)$, namely $\sum_{i\in V} g_i(0) < 0$ and $\sum_{i\in V} g_i(0) \geq 0$. The purpose of this section is to show that this distinction is only rough regarding the quantitative properties of $d_0(p)$. Namely, we use two examples to illustrate that the exact threshold value $d_0(p)$ varies with the graph structure and the location of sources and sinks.

The finer dependence of $d_0(p)$ on the graph structure should not be surprising. Theorem 1.1, grants the existence of a strictly increasing and continuous function $d_0(p)$ which acts as a threshold value for the diffusion rate above which there is local extinction present in the system (1.1). Lemma 3.1 and the analogue of Lemma 4.2 furthermore give us upper and lower bounds on $d_0(p)$, namely

$$\max_{i\in V} \frac{g_i(0)}{\deg(i)} \leq d_0(p) \leq \max_{i\in V} \frac{g_i(0)}{(1-p)\deg(i)}. \tag{6.1}$$

For example, for any fixed $n \geq 3$ and a vector $w \in \mathbb{R}^n$ any system (1.1) such that $\frac{g_i(0)}{\deg(i)} = w_i$ yields exactly the same lower and upper estimates for $d_0(p)$ via (6.1).

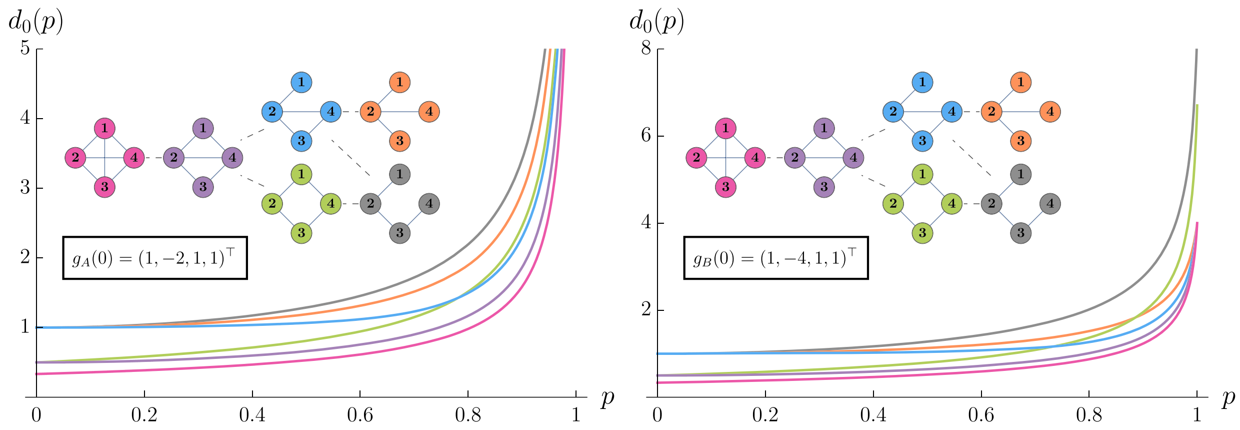



**Fig. 5.** Example of the threshold functions $d_0(p)$ for graphs $\mathcal{G}_i$, $i = 1, \dots 6$, defined in (6.2). The left panel depicts the case with the per capita growth rate vector $g_A(0) = (1, -2, 1, 1)^\top$. The right panel depicts the case with the per capita growth rate vector $g_B(0) = (1, -4, 1, 1)^\top$. (For interpretation of the colors in the figure(s), the reader is referred to the web version of this article.)

### 6.1. Graph structure

Let us consider all six undirected connected graphs with $n = 4$ vertices, i.e., $V(\mathcal{G}_i) = \{1, 2, 3, 4\}$ and

$$\begin{aligned} E(\mathcal{G}_1) &= \{\{1,2\},\{1,3\},\{1,4\},\{2,3\},\{2,4\},\{3,4\}\}, \\ E(\mathcal{G}_2) &= \{\{1,2\},\{1,4\},\{2,3\},\{2,4\},\{3,4\}\}, \\ E(\mathcal{G}_3) &= \{\{1,2\},\{2,3\},\{2,4\},\{3,4\}\}, \\ E(\mathcal{G}_4) &= \{\{1,2\},\{1,4\},\{2,3\},\{3,4\}\}, \\ E(\mathcal{G}_5) &= \{\{1,2\},\{2,3\},\{2,4\}\}, \\ E(\mathcal{G}_6) &= \{\{1,2\},\{2,3\},\{3,4\}\}, \end{aligned} \tag{6.2}$$

as in Fig. 5. One can consider the construction of $\mathcal{G}_i$ by a successive removal of edges starting with the complete graph $\mathcal{G}_1 = K_4$. We then distribute reaction rates such that there are three sources with per capita growth rate $g_i(0) = 1$, $i = 1, 3, 4$ and one sink located at the patch $i = 2$. We consider two cases; the sink has per capita growth rate either $g_2(0) = -2$ or $g_2(0) = -4$, see the left and right panels in Fig. 5, respectively. We denote the corresponding per capita growth rate vectors by $g_A(0) = (1, -2, 1, 1)^\top$ and $g_B(0) = (1, -4, 1, 1)^\top$. Note that

$$\sum_{i \in V} g_{A,i}(0) = 1 > 0 \qquad \text{and} \qquad \sum_{i \in V} g_{B,i}(0) = -1 < 0$$

and thus $\lim_{p \to 1^-} d_{0,A}(p) = \infty$ for each of the graphs $\mathcal{G}_i$ with $g_A(0)$ and $d_{0,B}(1) < \infty$ for $g_B(0)$ thanks to Theorem 1.1.

The reaction-degree distribution fully captures the properties of $d_0(p)$ only for $p = 0$ via Corollary 3.3. The continuity then extends the ordering for $p \approx 0$. It might seem that for given $p \in (0, 1)$ the value of $d_0(p)$ is negatively correlated with the number of edges. With fewer connections between patches it is easier to find almost isolated source which ensures the global persistence. In order to introduce extinction in the system, the diffusion rate must be high enough. Nevertheless, this does not provide the complete picture.

The intricate inner structure of the problem may be best illustrated by the case of the graphs $\mathcal{G}_1$, $\mathcal{G}_2$, $\mathcal{G}_3$ and $\mathcal{G}_5$ with the reaction $g_A(0)$. See the right panel of Fig. 5. The values $d_0(0)$ satisfy

$$d_{0,B}^{\mathcal{G}_1}(0) = \frac{g_{B,1}(0)}{\deg^{\mathcal{G}_1}(1)} = \frac{1}{3},$$

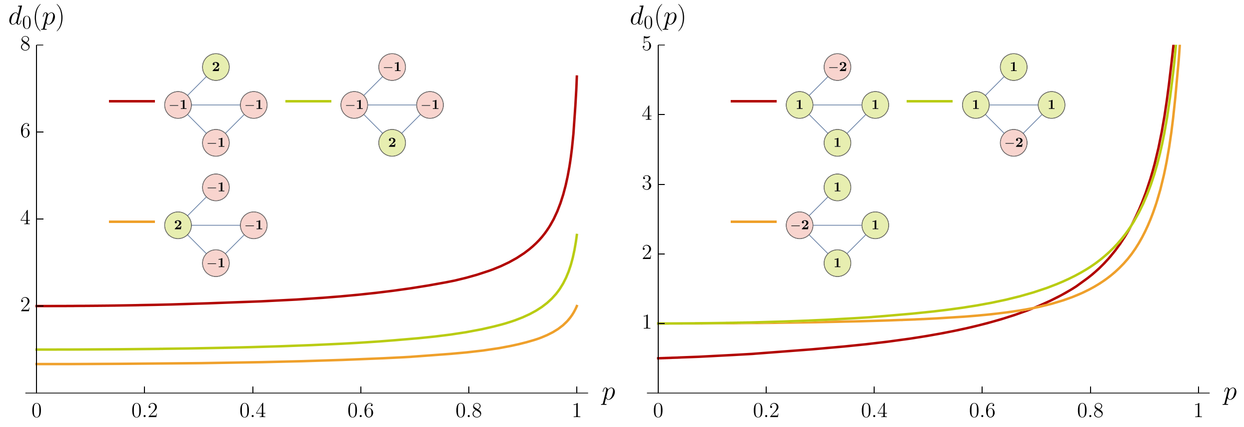



**Fig. 6.** The example of the functions $d_0(p)$ for a fixed graph $\mathcal{G}_3$ defined in (6.2) and two distinct distributions of the per capita growth rates $g_i(0)$. (For interpretation of the colors in the figure(s), the reader is referred to the web version of this article.)

$$d_{0,B}^{\mathcal{G}_2}(0) = \frac{g_{B,1}(0)}{\deg^{\mathcal{G}_2}(1)} = \frac{1}{2},$$

$$d_{0,B}^{\mathcal{G}_3}(0) = d_{0,B}^{\mathcal{G}_5}(0) = \frac{g_{B,1}(0)}{\deg^{\mathcal{G}_3}(1)} = \frac{1}{1} = 1,$$

see Corollary 3.3. On the other hand, it can be computed that

$$\lambda_{\max}(d,1) = \frac{1}{2}\left(-3 - 4d + \sqrt{25 + 20d + 16d^2}\right)$$

for all $\mathcal{G}_1$, $\mathcal{G}_2$, $\mathcal{G}_3$ and $\mathcal{G}_5$ and thus

$$d_{0,B}^{\mathcal{G}_1}(1) = d_{0,B}^{\mathcal{G}_2}(1) = d_{0,B}^{\mathcal{G}_3}(1) = d_{0,B}^{\mathcal{G}_5}(1) = 4.$$

## *6.2. Reaction distribution*

Let us now focus on the distribution sources and sinks. We focus on the graph $\mathcal{G}_3$ from Section 6.1 and two different scenarios. First, in the scenario $A$, we consider one source with per capita growth rate $g_i(0) = 2$ and three sinks with $g_i(0) = -1$. There exist three different configurations

$$g_{A_1}(0) = (2, -1, -1, -1)^\top,\ g_{A_2}(0) = (-1, 2, -1, -1)^\top,\ \text{and}\ g_{A_3}(0) = (-1, -1, 2, -1)^\top.$$

Note that the fourth possible configuration is identical to $g_{A_3}(0)$ since the patches 3 and 4 are interchangeable. In the second scenario denoted by $B$, there is one sink with per capita growth rate $g_i(0) = -2$ and three sources with $g_i(0) = 1$. Three distinct configurations are

$$g_{B_1}(0) = (-2, 1, 1, 1)^\top, \quad g_{B_2}(0) = (1, -2, 1, 1)^\top, \quad \text{and} \quad g_{B_3}(0) = (1, 1, -2, 1)^\top.$$

The functions for $d_0(p)$ for the respective cases are depicted in Fig. 6. In accordance with Theorem 1.1, $d_{0,A}(1) < \infty$ since $\sum_{i \in V} g_{A_j,i}(0) < 0$ for $j = 1, 2, 3$ and analogously, $d_{0,B}(1) = \infty$.

The first trivial observation is that the persistence-extinction properties of (1.1) vary with the change in the distribution of the per capita growth rates in a fixed graph. To conclude, no aggregate characteristics of the reaction vector $g(0)$ itself can fully describe the persistence-extinction behavior.

As in the previous case, the persistence in the system with a single source (the scenario $A$) tends to be stronger in the cases in which the source has fewer connection to other patches. Similar observation seems to be valid for the case of a single sink (the scenario $B$) and $p \approx 1$. Again, the well-connected sink tends to exterminate the population with higher rate of travel from the neighboring patches. This does not, however, hold for $p \approx 0$ in which the stability is mostly decided by the balance of the births at the sources and the almost-certain migration deaths.

## 7. Extensions

In this section we generalize our results for (1.1) to the case with an asymmetric dispersal and non-constant migration survival probabilities in the spirit of the previous studies by Freedman et al. [5] and Chen et al. [3], see (1.6)–(1.7). The main reason for the use of symmetric dispersal and constant migration survival probabilities in (1.1) was our focus on the dependence of the threshold value $d_0(p)$ on $p$ (see Theorem 1.1) and on the network structure (see Section 6). We extend these to the asymmetric model

$$u_i'(t) = d\left(\sum_{j\in\mathcal{N}^-(i)} p\, q_{ji} a_{ji} u_j(t) - \sum_{j\in\mathcal{N}^+(i)} a_{ij} u_i(t)\right) + u_i(t) g_i(u_i(t)), \tag{7.1}$$

which not only captures both (1.6) and (1.7) but also enables us to preserve our focus on the properties of $d_0(p)$.

The equation (7.1) describes dispersal and growth process on a weighted directed graph $\mathcal{G}_\mathrm{w}$ with weighted (asymmetric) adjacency matrix[1] $A_\mathrm{w} = (a_{ij}) \geq 0$. We assume that there are no self-loops and that $\mathcal{G}_\mathrm{w}$ is strongly connected. The overall dispersal rate is scaled by a scalar parameter $d > 0$. Each edge also has its intrinsic migration survival probability captured by $Q = (q_{ij}), q_{ij} \in [0, 1]$. In order to be able to control these probabilities we scale them with the parameter $p \in (0, 1]$ (similarly as $d$ scales $a_{ij}$). For the sake of consistency we require $\max(q_{ij}) = 1$ and $q_{ij} > 0$ if and only if $a_{ij} > 0$.

Let us define the sets of in- and out-neighbors $\mathcal{N}^-(i) = \{j \in V \mid a_{ji} > 0\}$ and $\mathcal{N}^+(i) = \{j \in V \mid a_{ij} > 0\}$. We can now rewrite (7.1) as

$$u'(t) = dp(A_\mathrm{w} \odot Q)^\top u(t) - dD_\mathrm{w}^+ u(t) + G(u(t))u(t), \tag{7.2}$$

in which $\odot$ is the Hadamard (elementwise) product and $D_\mathrm{w}^+ = \mathrm{diag}_{i\in V}\left(\sum_{j\in\mathcal{N}^+(i)} a_{ij}\right)$. The Jacobian at the origin is then

$$(F_\mathrm{w})_u'(0; d, p) = dp(A_\mathrm{w} \odot Q)^\top - dD_\mathrm{w}^+ + G(0).$$

The main difference in proving analogous statement to Theorem 1.1 now stems from the fact that the matrix $-(F_\mathrm{w})_u'(0; d, p)$ is not symmetric. The matrix is however a generalized graph Laplacian and the consequences of Lemma 2.1 hold. Thus, $\lambda_{\max} \in \mathbb{R}$ and the corresponding eigenvector $v_{\max} \in \mathbb{R}^n$ can be chosen such that $v_{\max,i} > 0$ for all $i \in V$. The linearized instability of the origin still implies uniform persistence – this follows either from a slight modification of Lemma 2.3 or from [14, Thm. 1 (ii)]. The maximal eigenvalue $\lambda_{\max}(d, p)$ is a continuous function of its parameters (the assumption of symmetry is not necessary in Lemma 2.6, see [9, Ch. 2]). The existence of the function $d_0(p)$ for $p \in (0, 1)$ follows from [3, Thm. 5.1]. Moreover, if $v_{\max}((A_\mathrm{w} \odot Q)^\top - D_\mathrm{w}^+)^\top (g_i(0))_{i\in V} < 0$ then the value $d_0(1)$ is finite. The continuity of $\lambda_{\max}(d, p)$ ensures that the function $d_0(p)$ is continuous, cf. Corollary 3.3 (i). It remains to show that the function $d_0(p)$ is strictly increasing as in Corollary 3.3 (ii). To this end we use the following consequence of Wielandt's theorem.

[1] Please note that our use of the standard graph-theoretical definition [6] of the asymmetric adjacency matrix $A_\mathrm{w}$ results in a different indexing of $a_{ij}$ in (7.1) in contrast to (1.6)–(1.7).

**Lemma 7.1** *([16, Cor. 2.2.1]). If $B$ is an irreducible matrix and $B \geq C \geq 0$, $B \neq C$, then $\lambda_{\max}(B) > \lambda_{\max}(C)$.*

Lemma 7.1 enables us to show a direct analogue of Corollary 2.11 (ii), i.e., that $\lambda_{\max}(d, \cdot)$ is strictly increasing.

**Lemma 7.2.** *The function $d_0(p)$ of $(F_{\mathrm{w}})'_u(0; d, p)$ is strictly increasing.*

**Proof.** In accordance with the proof of Corollary 3.3 (ii) it is sufficient to show that $\lambda_{\max}(d, \cdot)$ is strictly increasing for all $d > 0$, cf. Corollary 2.11 (ii).

Let $p = p^* + \Delta p$ be such that $p, \Delta p, p^* \in (0, 1)$, then

$$(F_{\mathrm{w}})'_u(0; d, p) = d\Delta p(A_{\mathrm{w}} \odot Q)^\top + (F_{\mathrm{w}})'_u(0; d, p^*).$$

The strong connectivity of the graph $\mathcal{G}_{\mathrm{w}}$ grants the irreducibility of $(F_{\mathrm{w}})'_u(0; d, p)$ and both $\lambda_{\max}(d, p^*)$, $\lambda_{\max}(d, p) \in \mathbb{R}$. In addition $(F_{\mathrm{w}})'_u(0; d, p^*) \leq (F_{\mathrm{w}})'_u(0; d, p)$ holds since $A_{\mathrm{w}} \odot Q$ is nonnegative.

There exists a constant diagonal matrix $E \geq 0$ such that $(F_{\mathrm{w}})'_u(0; d, p^*) + E$, $(F_{\mathrm{w}})'_u(0; d, p) + E \geq 0$. This operation merely shifts all eigenvalues by a constant step along real axis.

We get $\lambda_{\max}(d, p^*) < \lambda_{\max}(d, p)$ as a consequence of Lemma 7.1. □

These ideas can be seen as a sketch of the proof of the following statement equivalent to Theorem 1.1 for the asymmetric problem (7.1).

**Theorem 7.3.** *Consider the system* (7.1) *and assume that* (S) *is satisfied.*

1. *There exists a strictly increasing and continuous function $d_0(p)$, $d_0 : (0, 1) \to \mathbb{R}^+$, such that for a given $p \in (0, 1)$:*
   (i) *the system (7.1) is uniformly persistent provided $d \in (0, d_0(p))$,*
   (ii) *there is the local extinction in the system (7.1) provided $d > d_0(p)$.*
2. *If $v_{\max}((A_{\mathrm{w}} \odot Q)^\top - D^+)^\top (g_i(0))_{i \in V} < 0$ (cf. (7.2)), then there exists a finite $d_0(1) = \lim_{p \to 1^-} d_0(p)$ such that for $p = 1$:*
   (i) *the system (7.1) is uniformly persistent provided $d \in (0, d_0(1))$,*
   (ii) *there is the local extinction in the system (7.1) provided $d > d_0(1)$.*
3. *If $v_{\max}((A_{\mathrm{w}} \odot Q)^\top - D^+)^\top (g_i(0))_{i \in V} \geq 0$, then $\lim_{p \to 1^-} d_0(p) = \infty$ and the system (1.1) is uniformly persistent for $p = 1$ and every $d \in (0, \infty)$.*

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