

TWO NOVEL PROOFS OF SPECTRAL MONOTONICITY OF PERTURBED ESSENTIALLY NONNEGATIVE MATRICES WITH APPLICATIONS IN POPULATION DYNAMICS*

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Abstract. Threshold values in population dynamics can be formulated as spectral bounds of matrices, determining the dichotomy of population persistence and extinction. For a square matrix $\rho A + Q$, where A is an essentially nonnegative matrix describing population dispersal among patches in a heterogeneous environment and Q is a real diagonal matrix encoding within-patch population dynamics, the monotonicity of its spectral bound with respect to dispersal rate/coupling strength/travel frequency ρ has been established by Karlin and generalized by Altenberg while investigating the reduction principle in evolution biology and evolution dispersal in patchy landscapes. In this paper, we provide two new proofs rooted in our investigation of persistence in spatial population dynamics. The first one is an analytic derivation utilizing a graph-theoretic approach based on Kirchhoff's matrix-tree theorem; the second one employs the Collatz–Wielandt formula from matrix theory and complex analysis arguments. This monotonicity result has numerous applications in persistence and stability analysis of complex biological systems in heterogeneous environments. We illustrate this by applying it to well-known ecological models of single species, predator-prey, and competition.

Key words. spectral bound, Laplacian matrix, population persistence, population extinction, basic reproduction number, global stability, Karlin's theorem

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1. Introduction. Many complex systems in sciences and engineering can be modeled by coupled systems of differential equations on networks. A network can be mathematically treated as a weighted digraph (directed graph), consisting of a set of n vertices and a set of directed arcs. Specifically, within-vertex dynamics (when decoupled) are usually described by a small-scale system of differential equations, and a certain threshold parameter can often be determined to encode these dynamics. Directed arcs of the network represent the coupling among vertex systems, which can often be depicted as an essentially nonnegative matrix $A = (a_{ij})_{n \times n}$ with a nonpositive spectral bound, i.e., $s(A) := \max\{\operatorname{Re} \lambda : A x = \lambda x \text{ for some } x \in \mathbb{C}^n\} \leq 0$. In applications, A is often taken as the negative of a Laplacian matrix of the network. For example, in metapopulation dynamics, the essentially nonnegative matrix A represents the movement pattern of individuals among n geographical regions (or patches); specifically, $a_{ij} \geq 0$ ($i \neq j$) measures the movement of individuals from patch j to i ,

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and if individual loss during movement is neglected, then $a_{ii} = -\sum_{j \neq i} a_{ji}$ describes the total movement out from patch i . A linearization of such a coupled system at a certain equilibrium E_0 can often take (or be reduced to) the following form:

$$(1.1) \quad \frac{du_i(t)}{dt} = \rho \sum_{j=1}^n (a_{ij}u_j(t) - a_{ji}u_i(t)) + q_i u_i(t), \quad i = 1, \dots, n,$$

where $\rho > 0$ denotes the coupling strength. For examples in population dynamics, $u_i(t) \in \mathbb{R}_+$ denotes the population size at time t in the i th patch, $q_i \in \mathbb{R}$ represents the growth rate of the population in the i -patch, and the coupling strength ρ represents the movement rate of individuals between patches. Let $Q = \text{diag}(q_i)$ be a diagonal matrix; then the stability of the linear system (1.1) (thus the stability of E_0) depends on the spectral bound $s(\rho A + Q)$. For the population dynamics example, whether the metapopulation corresponds to system (1.1) is persistent or goes to extinction depends on whether the spectral bound is negative or positive, respectively. The linearized system (1.1) can also appear in other applications, such as interacting species in a patchy environment (see examples in section 5 and references therein), agreement and consensus problems in multiagent systems [35, 40], emergent behaviors in Cucker–Smale flocking [11, 37], and spatial spread of infectious diseases [8, 17, 18].

In this paper, we investigate the impact of the coupling strength ρ on the spectral bound $s(\rho A + Q)$ and thus on the dynamics of the coupled system. Specifically, we provide novel proofs of the following result and apply it to investigate the impact of the movement rates of species between patches on the population dynamics of several well-known ecological models.

THEOREM 1.1. *Let A be an essentially nonnegative irreducible matrix and let $Q = \text{diag}(q_i)$ be a real diagonal matrix. Then the following statements hold for $\rho \in (0, \infty)$:*

(i)

$$\frac{d}{d\rho} s(\rho A + Q) \leq s(A),$$

and the equality holds if and only if $q_1 = q_2 = \dots = q_n$. In particular, if $s(A) \leq 0$, then $s(\rho A + Q)$ is nonincreasing in ρ .

(ii)

$$\frac{d^2}{d\rho^2} s(\rho A + Q) \geq 0,$$

and the equality holds if and only if $q_1 = q_2 = \dots = q_n$.

Studies on the monotone dependence of $s(\rho A + Q)$ on ρ can be traced back to Karlin [25], in which, for an irreducible stochastic matrix P and a positive diagonal matrix R , $s(((1 - \rho)I + \rho P)R) = s(\rho(P - I)R + R)$ is proved to be strictly decreasing in ρ for $\rho \in (0, 1)$ unless R is a multiple of the identity matrix I . Karlin's theorem has been utilized in the mathematical generalization of the *reduction principle* [1, 3, 4, 15] in evolutionary biology: greater mixing reduces growth. While studying the evolution of dispersal in patchy landscapes, Kirkland, Li, and Schreiber [27] independently discovered Karlin's theorem with P being a substochastic matrix. Later, Altenberg [3] generalized Karlin's theorem to linear operators on Banach spaces, and Theorem 1.1 is the matrix version of Altenberg's result except that $s(\rho A + Q)$ is strictly convex in ρ in Altenberg's version while we will obtain the strict positivity of the second

derivative of $s(\rho A + Q)$ in ρ . Karlin's original proof in [25] uses the Donsker–Varadhan formula [13] for principal eigenvalues of essentially nonnegative matrices; Altenberg's proof in [3] relies on convex spectral functions due to Cohen [9], Friedland [16], and Kato [26]; the proof in [27] uses advanced matrix analysis techniques.

We will provide two novel proofs of the monotonicity of $s(\rho A + Q)$ on ρ . The first proof is for Theorem 1.1, which certainly is a problem of linear algebra, and comes from a graph-theoretic insight on coupled systems of ordinary differential equations on networks. Specifically, this graph-theoretic proof utilizes the α -weighted aggregation based on Kirchhoff's matrix-tree theorem and a tree-cycle identity, which has previously been used to construct global Lyapunov functions to successfully establish global dynamics for many coupled systems [30]. An alternative proof for part (i) of Theorem 1.1 is constructive and utilizes the “min-max” Collatz–Wielandt formula for the principal eigenvalue of nonnegative matrices.

By Theorem 1.1, if $s(A) \leq 0$, then the spectral bound $s(\rho A + Q)$ is monotonically decreasing from its maximum $\max_i \{q_i\}$ (as $\rho \rightarrow 0$) to a weighted average $\sum_i \alpha_i q_i$ (as $\rho \rightarrow \infty$). Here weight coefficients $\alpha_i \geq 0$ with $\sum_i \alpha_i = 1$ can be precisely determined by the underlying network structure. That is, as ρ decreases from ∞ to 0, the spectral bound increases monotonically and satisfies

$$(1.2) \quad \sum_i \alpha_i q_i \leq s(\rho A + Q) \leq \max_i \{q_i\}.$$

As a consequence, a strong coupling strength ρ tends to stabilize system (1.1), and thus a slow movement rate in metapopulation dynamics is in favor of population persistence. The former statement provides insight for the understanding of coupled systems of differential equations on networks, and the aggregation of the α -weighted average can be used to network/system design for better stabilized or controlled systems. The later statement agrees with previous results in spatial ecology and epidemiology on diffusion/dispersal rate, specially results on topics such as “the slower diffuser wins” [6, 12, 22, 31].

Our paper is organized as follows. In section 2, we state preliminaries and connections with Karlin's theorem. In sections 3 and 4, we provide two different proofs for the monotonicity of $s(\rho A + Q)$. In section 5, we apply Theorem 1.1 to some population models from ecology and highlight the impact of the movement rates of species between patches on the population dynamics.

2. Preliminary. Let A be an $n \times n$ matrix and let $\sigma(A)$ be the set of eigenvalues of A . Let $r(A)$ be the *spectral radius* of A , i.e.,

$$r(A) = \max\{|\lambda| : \lambda \in \sigma(A)\}.$$

Let $s(A)$ be the *spectral bound* (also called *spectral abscissa*) of A , i.e.,

$$s(A) = \max\{\operatorname{Re} \lambda : \lambda \in \sigma(A)\}.$$

A vector $u \gg 0$ means that every entry of u is positive. Let I denote the $n \times n$ identity matrix.

A square matrix is called *stochastic* if all the entries are nonnegative and every column adds up to 1. Let $A = (a_{ij})_{n \times n}$ be a square matrix; A is called an *M-matrix* if $a_{ij} \leq 0$ for all $i \neq j$ and $A = sI - B$ with B having all off-diagonal elements nonnegative and $s \geq r(B)$; A is called *essentially nonnegative* (also called the *Metzler matrix*) if $a_{ij} \geq 0$ for all $i \neq j$. The connection between *M*-matrices and essentially

nonnegative matrices can be viewed through the following well-known results: $-A$ is a nonsingular (singular) M -matrix if and only if A is essentially nonnegative with $s(A) < 0$ ($s(A) = 0$); if A is a singular M -matrix, then $A + D$ is a nonsingular M -matrix for any diagonal matrix $D = \text{diag}(d_i)$ with $d_i > 0$ for all i .

A square matrix L is called a *Laplacian* matrix if all the off-diagonal entries are nonpositive and the sum of each column is zero. If L is a Laplacian matrix, it is easy to see that $(1, 1, \dots, 1)$ is a left eigenvector of L corresponding to the eigenvalue 0. In our applications to spatial population dynamics, the Laplacian matrix encodes all movement between patches and no population loss is assumed during the dispersal. For our purpose, a square matrix $L = (\ell_{ij})$ is called *sub-Laplacian* if $\ell_{ij} \leq 0$ for all $i \neq j$ and $\ell_{jj} \geq -\sum_{i \neq j} \ell_{ij}$ for all j . A sub-Laplacian matrix L is called *strongly (strictly) sub-Laplacian* if $\ell_{jj} > -\sum_{i \neq j} \ell_{ij}$ for all (some) j . Sub-Laplacian matrices defined above allow us to include possible population loss during the dispersal in our studies; see, for example, section 5.1.

In [25], Karlin proved the following theorem on the monotonicity of the spectral radii of a family of matrices, which was interpreted as the mathematical explanation of the *reduction principle* [3, 15] in evolution biology. Karlin's proof relies on the Donsker–Varadhan formula for the principal eigenvalue. Later, this result was discovered independently by Kirkland, Li, and Schreiber [27] (see also [36]), and their proof is based on techniques of matrix analysis.

THEOREM 2.1 (Karlin's theorem). *Let P be an irreducible stochastic matrix. Consider the family of matrices $P_\rho = (1 - \rho)I + \rho P$ with $0 < \rho < 1$. Then for any diagonal matrix $R = \text{diag}(r_i)$ with $r_i > 0$ for all i , $r(P_\rho R)$ is strictly decreasing in ρ provided that R is not a multiple of I .*

Theorem 2.1 has been applied to the following discrete time linear population model [25]:

$$(2.1) \quad x(t+1) = [(1 - \rho)I + \rho P]Rx(t).$$

Here, $x(t)$ is a vector-valued function denoting the frequency of a rare allele in each subdivision of some population (e.g., genotypes); R is a real diagonal matrix measuring the growth rate of a rare allele in each subdivision; stochastic matrix P represents the pattern of dispersal; ρ is the rate of dispersal (or mutation, mixing, etc.). The spectral radius $r(P_\rho R)$ measures the growth rate of a rare allele in the population. Biologically, Theorem 2.1 implies that smaller rates of dispersal favor the evolutionary protection of a rare allele.

To view the connection between the spectral radius problem on (2.1) and our spectral bound problem on (1.1), we set $P_\rho R = \rho(P - I)R + R = \rho A + R$, where $A = (P - I)R$ is an essentially nonnegative matrix. The corresponding continuous-time version of model (2.1) can be written as

$$x'(t) = [\rho A + Q]x(t),$$

where $Q = R - I$ is a real diagonal matrix representing the growth rate of each subdivision, but the diagonal entry $q_i = r_i - 1$ of Q is not necessarily positive. Since A is essentially nonnegative, it generates a positive semigroup $\text{Exp}(tA)$, measuring the dispersal (or mutation, mixing, etc.) between subdivisions. The impact of dispersal rate ρ has been shown in the following theorem, which is a generalization of Theorem 2.1.

THEOREM 2.2 (Altenberg [2, 3]). *Let A be an irreducible essentially nonnegative matrix and let Q be a real diagonal matrix. Consider the family of matrices $M(\rho) = \rho A + Q$ with $\rho > 0$. Then*

1. $s(M(\rho))$ is either a constant or strictly decreasing in $\rho \in (0, \infty)$ if $s(A) \leq 0$, and moreover,

$$\frac{d}{d\rho}s(M(\rho)) \leq s(A),$$

and the equality holds if and only if Q is a multiple of I ;

2. $s(M(\rho))$ is convex in ρ , i.e., for any $0 < \alpha < 1$, and $\rho_1, \rho_2 \geq 0$ with $\rho_1 \neq \rho_2$,

$$s((1 - \alpha)M(\rho_1) + \alpha M(\rho_2)) \leq (1 - \alpha)s(M(\rho_1)) + \alpha s(M(\rho_2)),$$

and the equality holds if and only if Q is a multiple of I .

Theorems 1.1 and 2.2 are the same except that the second derivative of $s(\rho A + Q)$ is strictly positive if Q is not a multiple of I in Theorem 1.1 while $s(\rho A + Q)$ is strictly convex in ρ in Theorem 2.2. Theorem 2.2 can be used to prove Theorem 2.1 (see the proof at the end of this section). We remark that the original statement of Theorem 2.2 in [3] is for operators on Banach spaces. Altenberg's proof is based on the convexity of the spectral radius due to Cohen [9] and Kato [26].

Finally we prove that Theorem 2.2 implies Theorem 2.1. In the next two sections, we give two proofs of strengthened versions of Theorem 2.2, which also lead to new proofs of Theorem 2.1.

Proof of Theorem 2.1 from Theorem 2.2. Since P is an irreducible stochastic matrix, $P_\rho = (1 - \rho)I + \rho P = I - \rho(I - P)$ is a nonnegative irreducible matrix. Hence, $P_\rho R = R - \rho(I - P)R$ is nonnegative as R is positive. It follows from the Perron–Frobenius theory that $r(P_\rho R) = s(P_\rho R)$. On the other hand, all off-diagonal entries of $(I - P)R$ are nonpositive, and the sum of entries of each column of $(I - P)R$ is zero. Hence $(I - P)R$ is a Laplacian matrix, and thus $A = -(I - P)R$ is essentially nonnegative with $s(A) = 0$. Notice that A is also irreducible since P is irreducible. Therefore, by Theorem 2.2, $r(P_\rho R) = s(P_\rho R)$ is strictly decreasing in z provided that R is not a multiple of I . $\square$

3. A graph theoretical proof of Theorem 1.1. In this section, we apply a graph-theoretic approach to prove Theorem 1.1. The terminology and results from graph theory can be found in the appendix.

Let A be an essentially nonnegative matrix and Q be a diagonal matrix. If A is irreducible, then $\rho A + Q$ is irreducible and, by the Perron–Frobenius theorem, $s(\rho A + Q)$ is the principal eigenvalue of $\rho A + Q$, which is simple and associated with a positive eigenvector. To study the spectral bound $s(\rho A + Q)$, we start by the case that $-A$ is Laplacian and consider the weighted directed graph with n vertices associated with $-A$.

THEOREM 3.1. *Let A be an irreducible essentially nonnegative matrix such that $-A$ is a Laplacian matrix, and let $Q = \text{diag}(q_i)$ be a real diagonal matrix. Denote $M(\rho) = \rho A + Q$. Then for any $\rho > 0$,*

(i)

$$(3.1) \quad \frac{d}{d\rho}s(M(\rho)) \leq 0,$$

and the equality holds if and only if $q_1 = q_2 = \cdots = q_n$;

(ii)

$$(3.2) \quad \frac{d^2}{d\rho^2} s(M(\rho)) \geq 0,$$

and the equality holds if and only if $q_1 = q_2 = \cdots = q_n$.

Proof. By the Perron–Frobenius theorem, $s(M(\rho))$ is the principal eigenvalue of $M = M(\rho)$. Denote $\lambda^* = s(M) = s(M^T)$, where M^T is the transpose of M . Since M^T is essentially nonnegative and irreducible, λ^* is an eigenvalue of M^T with corresponding eigenvector $w = (w_1, w_2, \dots, w_n)^T$ with $w_j > 0$ for all j . Notice that w_i and λ^* depend smoothly on ρ . Without loss of generality, we assume that $\sum_{i=1}^n w_i = 1$ for any $\rho > 0$, which implies that (here $'$ is the derivative with respect to ρ)

$$(3.3) \quad \sum_{i=1}^n w'_i = 0.$$

Since Q is diagonal, $M^T = \rho A^T + Q$. Hence, for each i ,

$$(3.4) \quad \lambda^* w_i = q_i w_i - \rho \sum_{j \neq i} a_{ji} w_i + \rho \sum_{j \neq i} a_{ji} w_j.$$

We first prove (i). Differentiating (3.4) with respect to ρ yields

$$(3.5) \quad (\lambda^*)' w_i + \lambda^* w'_i = q_i w'_i - \sum_{j \neq i} a_{ji} w_i - \rho \sum_{j \neq i} a_{ji} w'_i + \sum_{j \neq i} a_{ji} w_j + \rho \sum_{j \neq i} a_{ji} w'_j.$$

Multiplying (3.5) by w_i gives

$$(3.6) \quad (\lambda^*)' w_i^2 + \lambda^* w'_i w_i = q_i w'_i w_i + \sum_{j \neq i} a_{ji} (w_j - w_i) w_i + \rho \sum_{j \neq i} a_{ji} (w'_j - w'_i) w_i.$$

By substituting (3.4) into the second term of (3.6), we obtain

$$(3.7) \quad (\lambda^*)' w_i^2 = \sum_{j \neq i} a_{ji} w_j w_i \left(1 - \frac{w_i}{w_j} \right) + \rho \sum_{j \neq i} a_{ji} w_j w_i \left(\frac{w'_j}{w_j} - \frac{w'_i}{w_i} \right).$$

Now set $B = (b_{ij})_{n \times n}$ with $b_{ij} = a_{ij} w_i w_j$ for $1 \leq i, j \leq n$. Let θ_i be the cofactor of the i th diagonal entry of the Laplacian matrix corresponding to B for $1 \leq i \leq n$. Multiplying (3.7) by θ_i and summing these over all i yield

$$(3.8) \quad (\lambda^*)' \sum_{i=1}^n \theta_i w_i^2 = \sum_{i=1}^n \sum_{j \neq i} \theta_i b_{ji} \left[1 - \frac{w_i}{w_j} + \rho \left(\frac{w'_j}{w_j} - \frac{w'_i}{w_i} \right) \right].$$

It follows from the tree-cycle identity (see Theorem A.1 in the appendix, and here we choose $x_i = (w_i, w'_i)$ and $F_{ji}(x_j, x_i) = 1 - \frac{w_i}{w_j} + \rho(\frac{w'_j}{w_j} - \frac{w'_i}{w_i})$) that

$$(3.9) \quad \begin{aligned} \sum_{i=1}^n \sum_{j \neq i} \theta_i b_{ji} \left[1 - \frac{w_i}{w_j} + \rho \left(\frac{w'_j}{w_j} - \frac{w'_i}{w_i} \right) \right] \\ = \sum_{Q \in \mathcal{Q}} w(Q) \sum_{(s,r) \in E(C_Q)} \left[1 - \frac{w_s}{w_r} + \rho \left(\frac{w'_r}{w_r} - \frac{w'_s}{w_s} \right) \right], \end{aligned}$$

where $\mathcal{Q}$ is the set of all spanning unicycle graphs of $(\mathcal{G}_B, B)$, $w(\mathcal{Q}) > 0$ is the weight of $\mathcal{Q}$, and $\mathcal{C}_{\mathcal{Q}}$ denotes the directed cycle of $\mathcal{Q}$ with directed edge set $E(\mathcal{C}_{\mathcal{Q}})$. Along any directed cycle $\mathcal{C}_{\mathcal{Q}}$ of length l ,

$$\begin{aligned} \sum_{(s,r) \in E(\mathcal{C}_{\mathcal{Q}})} \left(1 - \frac{w_s}{w_r}\right) &= l - \left(\sum_{(s,r) \in E(\mathcal{C}_{\mathcal{Q}})} \frac{w_s}{w_r} \right) \\ (3.10) \quad &\leq l - l \cdot \left(\prod_{(s,r) \in E(\mathcal{C}_{\mathcal{Q}})} \frac{w_s}{w_r} \right)^{1/l} = l - l \cdot 1 = 0. \end{aligned}$$

Here we use the inequality of arithmetic and geometric means (AM-GM) $(x_1 + x_2 + \cdots + x_l)/l \geq \sqrt[l]{x_1 x_2 \cdots x_l}$ and

$$(3.11) \quad \sum_{(s,r) \in E(\mathcal{C}_{\mathcal{Q}})} \left(\frac{w'_r}{w_r} - \frac{w'_s}{w_s} \right) = 0.$$

Combining (3.8)–(3.11) yields $(\lambda^*)' \leq 0$. Notice that $(\lambda^*)' = 0$ if and only if the equality holds in (3.10) for any directed cycle, that is, $w_r = w_s$ for any pair of (s, r) locating in a directed cycle of $(\mathcal{G}_B, B)$. Since B is irreducible, $(\mathcal{G}_B, B)$ is strongly connected. As a consequence, $w_i = w_j$ for any i, j . Substituting these into (3.4) yields $\lambda^* = q_i$ for all i , which completes the proof of (i).

Next we prove (ii). In the following $''$ is the second derivative with respect to ρ . Differentiating (3.5) with respect to ρ yields

$$\begin{aligned} (3.12) \quad (\lambda^*)'' w_i + 2(\lambda^*)' w'_i + \lambda^* w''_i \\ = q_i w''_i - 2 \sum_{j \neq i} a_{ji} w'_i - \rho \sum_{j \neq i} a_{ji} w''_i + 2 \sum_{j \neq i} a_{ji} w'_j + \rho \sum_{j \neq i} a_{ji} w''_j. \end{aligned}$$

Multiplying (3.12) by w_i gives

$$\begin{aligned} (3.13) \quad (\lambda^*)'' w_i^2 + 2(\lambda^*)' w'_i w_i + \lambda^* w''_i w_i \\ = q_i w_i w''_i - 2 \sum_{j \neq i} a_{ji} w'_i w_i - \rho \sum_{j \neq i} a_{ji} w''_i w_i + 2 \sum_{j \neq i} a_{ji} w'_j w_i + \rho \sum_{j \neq i} a_{ji} w''_j w_i. \end{aligned}$$

Substituting (3.4) and (3.7) into (3.13), we have

$$\begin{aligned} (\lambda^*)'' w_i^2 &= \rho \sum_{j \neq i} a_{ji} w_j w_i \left(\frac{w''_j}{w_j} - \frac{w''_i}{w_i} \right) + 2 \sum_{j \neq i} a_{ji} w_j w_i \left(\frac{w'_j}{w_j} - \frac{w'_i}{w_i} \right) \\ (3.14) \quad &- 2\rho \sum_{j \neq i} a_{ji} w_j w_i \left[\frac{w'_j}{w_j} \frac{w'_i}{w_i} - \left(\frac{w'_i}{w_i} \right)^2 \right]. \end{aligned}$$

Recall $b_{ij} = a_{ij} w_i w_j$. Multiplying (3.7) by θ_i and summing these over all i yields

$$\begin{aligned} (\lambda^*)'' \sum_{i=1}^n \theta_i w_i^2 \\ (3.15) \quad = \sum_{i=1}^n \sum_{j \neq i} \theta_i b_{ji} \left[\rho \left(\frac{w''_j}{w_j} - \frac{w''_i}{w_i} \right) + 2 \left(\frac{w'_j}{w_j} - \frac{w'_i}{w_i} \right) - 2\rho \left(\frac{w'_j}{w_j} \frac{w'_i}{w_i} - \left(\frac{w'_i}{w_i} \right)^2 \right) \right]. \end{aligned}$$

It follows from the tree-cycle identity (see Theorem A.1 in the appendix, and here we choose $x_i = (w_i, w'_i, w''_i)$ and $F_{ji}(x_j, x_i) = \rho(\frac{w''_j}{w_j} - \frac{w''_i}{w_i}) + 2(\frac{w'_j}{w_j} - \frac{w'_i}{w_i}) - 2\rho(\frac{w'_j w'_i}{w_j w_i} - (\frac{w'_i}{w_i})^2)$), (3.11), and (3.11) type equality for w''_j/w_j that

$$\begin{aligned} (3.16) \quad & (\lambda^*)'' \sum_{i=1}^n \theta_i w_i^2 \\ &= \sum_{\mathcal{Q} \in \mathcal{Q}} w(\mathcal{Q}) \sum_{(s,r) \in E(\mathcal{C}_{\mathcal{Q}})} \left[\rho \left(\frac{w''_r}{w_r} - \frac{w''_s}{w_s} \right) + 2 \left(\frac{w'_r}{w_r} - \frac{w'_s}{w_s} \right) - 2\rho \left(\frac{w'_r w'_s}{w_r w_s} - \left(\frac{w'_s}{w_s} \right)^2 \right) \right] \\ &= \rho \sum_{\mathcal{Q} \in \mathcal{Q}} w(\mathcal{Q}) \sum_{(s,r) \in E(\mathcal{C}_{\mathcal{Q}})} \left(\frac{w'_r}{w_r} - \frac{w'_s}{w_s} \right)^2 \geq 0. \end{aligned}$$

Notice that $(\lambda^*)'' = 0$ if and only if $\frac{w'_r}{w_r} = \frac{w'_s}{w_s}$ for any pair of (s, r) locating in a directed cycle of $(\mathcal{G}_B, B)$. Since B is irreducible, the graph $(\mathcal{G}_B, B)$ is strongly connected. As a consequence, $\frac{w'_i}{w_i} = \frac{w'_j}{w_j}$ for any i, j . Therefore, $w'_i = kw_i$ for all i for some $k \in \mathbb{R}$. This, combined with (3.3) and $w_i > 0$, implies that $w'_i = 0$ for any $i = 1, \dots, n$. Substituting $w'_i = 0$ into (3.5), we have

$$(\lambda^*)' w_i = - \sum_{j \neq i} a_{ji} w_i + \sum_{j \neq i} a_{ji} w_j,$$

which implies that $(\lambda^*)'$ is the principal eigenvalue of A^T and therefore $(\lambda^*)' = 0$. From (i) we see that $\lambda^* = q_i$ for all i , and (ii) holds. $\square$

In Theorem 3.1, the column sum of the matrix A is zero which represents that the dispersal has no loss of population. A slightly stronger result holds when there is a loss of population when dispersing. Since Corollary 3.2 follows directly from Theorem 1.1, we omit its proof. We remark that Corollary 3.2(ii) provides a new equality condition on an earlier result in [2, Corollary 8].

COROLLARY 3.2. *Let A be an irreducible essentially nonnegative matrix such that $-A$ is a strictly sub-Laplacian matrix, and let $Q = \text{diag}(q_i)$ be a real diagonal matrix. Denote $M(\rho) = \rho A + Q$. Then for any $\rho > 0$,*

(i)

$$\frac{d}{d\rho} s(M(\rho)) < 0,$$

(ii)

$$\frac{d^2}{d\rho^2} s(M(\rho)) \geq 0,$$

and the equality holds if and only if $q_1 = q_2 = \dots = q_n$.

Now we are ready to prove Theorem 1.1 using Theorem 3.1.

Proof of Theorem 1.1. First we assume that $s(A) = 0$. Since A is an irreducible essentially nonnegative matrix, by the Perron–Frobenius theorem, A has a left principal eigenvector $u = (u_1, u_2, \dots, u_n)^T \gg 0$ corresponding with eigenvalue $s(A)$. Denote $U = \text{diag}(u_i)$ and $\tilde{A} = UAU^{-1}$. Since $s(A) = 0$, $-\tilde{A}$ is a Laplacian matrix.

Indeed since $UAU^{-1} = (u_i a_{ij} u_j^{-1})$, the matrix UAU^{-1} is essentially nonnegative and the sum of the j th column is $u_j^{-1} \sum_{i=1}^n u_i a_{ij} = s(A) u_j^{-1} u_j = s(A)$. If $s(A) = 0$, then the sum of each column of UAU^{-1} is zero and $-UAU^{-1}$ is a Laplacian matrix. Since $s(\rho A + Q) = s(U(\rho A + Q)U^{-1}) = s(\rho \tilde{A} + Q)$, the results follow from Theorem 3.1.

If $s(A) \neq 0$, we replace A by $A - s(A)I$ to obtain

$$\frac{d}{d\rho} s(\rho A + Q) \leq s(A) \quad \text{and} \quad \frac{d^2}{d\rho^2} s(\rho A + Q) \geq 0,$$

and the equality holds if and only if $q_1 = q_2 = \cdots = q_n$. $\square$

The nonincreasing property of the spectral bound of irreducible matrices as established in Theorem 1.1 also holds for reducible matrices. The following result was previously established in [2, Theorem 6].

COROLLARY 3.3. *Let A be an essentially nonnegative matrix with $s(A) \leq 0$, and let $Q = \text{diag}(q_i)$ be a real diagonal matrix. Then $s(\rho A + Q)$ is nonincreasing and convex for all $\rho > 0$.*

Proof. The eigenvalues and spectral bound of A are invariant under permutation similarity transformation $P^{-1}AP$ for a permutation matrix P . So without loss of generality, we can assume that A is a block upper triangular matrix:

$$A = \begin{bmatrix} B_1 & * & \cdots & * \\ 0 & B_2 & \cdots & * \\ \cdots & \cdots & \cdots & \cdots \\ 0 & 0 & \cdots & B_k \end{bmatrix},$$

where B_i ($1 \leq i \leq k$) are $p_i \times p_i$ irreducible essentially nonnegative matrices with size $p_i \geq 1$ and $\sum_{i=1}^k p_i = n$. We also break $Q = \text{diag}(q_i)$ to match with the size of A : $Q = \text{diag}(Q_i)$, where Q_i is a real diagonal matrix of size $p_i \times p_i$. Apparently $s(\rho A + Q) = \max\{s(\rho B_i + Q_i) : 1 \leq i \leq k\}$.

Since for each i , $s(\rho B_i + Q_i)$ is nonincreasing and convex in ρ from Theorem 1.1, we conclude that $s(\rho A + Q)$ is also nonincreasing and convex in ρ as the maximum of a finite number of nonincreasing and convex functions. Indeed we can have the strict inequality if either (i) $s(\rho A + Q) = s(\rho B_i + Q_i)$ for a fixed $1 \leq i \leq k$ and $Q_i \neq cI_i$ for any $c \in \mathbb{R}$ and I_i is the $p_i \times p_i$ identity matrix, or (ii) for each $1 \leq i \leq k$, $Q_i \neq cI_i$ for any $c \in \mathbb{R}$. In either case, the strict inequality follows from Theorem 1.1. $\square$

One may suspect that the graph theoretical method can be used to show that the third derivative of $s(\rho A + Q)$ is negative or positive. However, from the following example, we can see that the third derivative may not be of one sign. Let

$$A = \begin{pmatrix} -\frac{1}{2} & 1 \\ \frac{1}{2} & -1 \end{pmatrix} \quad \text{and} \quad Q = \begin{pmatrix} 1 & 0 \\ 0 & 2 \end{pmatrix}.$$

Then we can compute

$$s(\rho) := s(\rho A + Q) = \frac{6 - 3\rho + \sqrt{9\rho^2 - 4\rho + 4}}{4}.$$

From elementary calculation, we can see that $s(\rho) > 0$, $s'(\rho) < 0$, and $s''(\rho) > 0$ for all $\rho > 0$, which is in agreement with Theorem 3.1. But the third derivative $s^{(3)}(\rho)$ changes sign.

4. A constructive proof of Theorem 1.1. In this section, we provide a constructive method to prove part (i) of Theorem 1.1. Our proof is based on the “min-max” Collatz–Wielandt formula [33, section 8.2]:

$$s(A) = \min_{u \gg 0} \max_{1 \leq i \leq n} \frac{[Au]_i}{[u]_i},$$

where $A = (a_{ij})_{n \times n}$ is a nonnegative irreducible matrix. Notice that if A is essentially nonnegative and irreducible, then $A + kI$ is nonnegative irreducible if k is large. Using this, it is easy to see that this formula also holds for essentially nonnegative irreducible matrices. Our method to prove that $s(\rho A + Q)$ is decreasing in ρ is elementary, and then we utilize theory from complex analysis to prove that $s(\rho A + Q)$ is strictly decreasing: the zeros of analytic functions are isolated.

The following elementary algebra lemma is essential for the proof of monotonicity of $s(\rho A + Q)$, which may be of independent interest.

LEMMA 4.1. *Let $\rho, \rho', u_i > 0$, $i = 1, 2, \dots, n$. Suppose $u_i \neq u_j$, for all $i \neq j$, where $i, j = 1, 2, \dots, n$. Then there exist $k_i > 0$, $i = 1, 2, \dots, n$, such that*

$$(4.1) \quad \frac{u_j(\rho + \rho')}{\rho' u_i + \rho u_j} < \frac{k_i}{k_j} < \frac{\rho' u_j + \rho u_i}{u_i(\rho + \rho')} \quad \forall i \neq j, \quad i, j = 1, 2, \dots, n.$$

Proof. Without loss of generality, we may assume $u_1 < u_2 < \dots < u_n$. First, we show that (4.1) makes sense, i.e.,

$$(4.2) \quad \frac{u_j(\rho + \rho')}{\rho' u_i + \rho u_j} < \frac{\rho' u_j + \rho u_i}{u_i(\rho + \rho')}.$$

Equation (4.2) is equivalent to

$$u_i u_j (\rho + \rho')^2 < (\rho' u_i + \rho u_j)(\rho' u_j + \rho u_i),$$

which can be simplified as

$$2u_i u_j < u_i^2 + u_j^2.$$

Since $u_i \neq u_j$, (4.2) is true.

Now we construct $k_1, k_2, \dots, k_n$. Let $k_1 = 1$. We choose $k_i > 0$, $i \geq 2$, recursively, such that

$$(4.3) \quad \frac{u_i(\rho + \rho')}{\rho' u_{i+1} + \rho u_i} < \frac{k_{i+1}}{k_i} < \frac{\rho' u_i + \rho u_{i+1}}{u_{i+1}(\rho + \rho')}, \quad i = 1, 2, \dots, n-1.$$

We only need to prove that k_i , $i = 1, 2, \dots, n$, satisfy (4.1).

We claim that

$$(4.4) \quad \frac{u_i(\rho + \rho')}{\rho' u_{i+2} + \rho u_i} < \frac{k_{i+2}}{k_i} < \frac{\rho' u_i + \rho u_{i+2}}{u_{i+2}(\rho + \rho')}, \quad i = 1, 2, \dots, n-2.$$

To see this, by (4.3),

$$(4.5) \quad \frac{u_{i+1}(\rho + \rho')}{\rho' u_{i+2} + \rho u_{i+1}} < \frac{k_{i+2}}{k_{i+1}} < \frac{\rho' u_{i+1} + \rho u_{i+2}}{u_{i+2}(\rho + \rho')}.$$

Multiplying (4.3) and (4.5), we obtain

$$(4.6) \quad \frac{u_i(\rho + \rho')}{\rho' u_{i+1} + \rho u_i} \frac{u_{i+1}(\rho + \rho')}{\rho' u_{i+2} + \rho u_{i+1}} < \frac{k_{i+2}}{k_i} < \frac{\rho' u_i + \rho u_{i+1}}{u_{i+1}(\rho + \rho')} \frac{\rho' u_{i+1} + \rho u_{i+2}}{u_{i+2}(\rho + \rho')}.$$

To show (4.4), it suffices to prove that

$$(4.7) \quad \frac{u_i(\rho + \rho')}{\rho' u_{i+2} + \rho u_i} < \frac{u_i(\rho + \rho')}{\rho' u_{i+1} + \rho u_i} \frac{u_{i+1}(\rho + \rho')}{\rho' u_{i+2} + \rho u_{i+1}}$$

and

$$\frac{d' u_i + \rho u_{i+1}}{u_{i+1}(\rho + \rho')} \frac{\rho' u_{i+1} + \rho u_{i+2}}{u_{i+2}(\rho + \rho')} < \frac{\rho' u_i + \rho u_{i+1}}{u_{i+2}(\rho + \rho')}.$$

These two inequalities can be checked directly. We only show (4.7), as the other is similar. Equation (4.7) is equivalent to

$$(\rho' u_{i+1} + \rho u_i)(\rho' u_{i+2} + \rho u_{i+1}) < (\rho' u_{i+2} + \rho u_i) u_{i+1}(\rho + \rho'),$$

which can be simplified as

$$\rho' \rho (u_{i+1}^2 + u_i u_{i+2}) < \rho' \rho (u_{i+1} u_{i+2} + u_i u_{i+1}).$$

This is equivalent to

$$\rho' \rho (u_{i+1} - u_{i+2})(u_{i+1} - u_i) < 0,$$

which holds as $u_i < u_{i+1} < u_{i+2}$. This proves (4.4).

By (4.3) and (4.4), we can show that

$$(4.8) \quad \frac{u_i(\rho + \rho')}{\rho' u_{i+3} + \rho u_i} < \frac{k_{i+3}}{k_i} < \frac{\rho' u_i + \rho u_{i+3}}{u_{i+3}(\rho + \rho')}, \quad i = 1, 2, \dots, n-3.$$

The proof of (4.8) is similar to (4.4). Indeed, by (4.3), we have

$$\frac{u_{i+2}(\rho + \rho')}{\rho' u_{i+3} + \rho u_{i+2}} < \frac{k_{i+3}}{k_{i+2}} < \frac{\rho' u_{i+2} + \rho u_{i+3}}{u_{i+3}(\rho + \rho')}.$$

Multiplying this inequality with (4.4), we can show (4.8). Then by induction, we can show that

$$(4.9) \quad \frac{u_i(\rho + \rho')}{\rho' u_{i+j} + \rho u_i} < \frac{k_{i+j}}{k_i} < \frac{\rho' u_i + \rho u_{i+j}}{u_{i+j}(\rho + \rho')}, \quad i = 1, 2, \dots, n-j, \quad j = 1, 2, \dots, n.$$

This proves (4.1). $\square$

In the following, we prove part (i) of Theorem 1.1 via several steps. First we show that $s(\rho A + Q)$ is nonincreasing.

LEMMA 4.2. *Let $A = (a_{ij})_{n \times n}$ be an irreducible essentially nonnegative matrix such that $-A^T$ is sub-Laplacian, and let $Q = \text{diag}(q_i)$ be a real diagonal matrix. Then $s(\rho A + Q)$ is nonincreasing in $\rho \in (0, \infty)$. If, in addition, $-A^T$ is strongly sub-Laplacian, then $s(\rho A + Q)$ is strictly decreasing in $\rho \in (0, \infty)$.*

Proof. By the Perron–Frobenius theorem, $A_\rho := \rho A + Q$ has a positive eigenvector $u = (u_1, u_2, \dots, u_n)^T$ corresponding with eigenvalue $\lambda_1 = s(A_\rho)$. Then, we have

$$(4.10) \quad q_i u_i + \rho \sum_{j=1}^n a_{ij} u_j = \lambda_1 u_i, \quad i = 1, 2, \dots, n.$$

For any $\rho' > 0$, to show $s(A_{\rho+\rho'}) \leq s(A_\rho)$, by the Collatz–Wielandt formula, it suffices to find a strictly positive vector $v = (v_1, v_2, \dots, v_n)^T$ such that

$$(4.11) \quad \max_{1 \leq i \leq n} \frac{[A_{\rho+\rho'}v]_i}{[v]_i} \leq \lambda_1.$$

Suppose $v_i = k_i u_i$ for some $k_i > 0$, $i = 1, 2, \dots, n$. We need to find k_i satisfying (4.11), i.e.,

$$(4.12) \quad \frac{q_i k_i u_i + (\rho + \rho') \sum_{j=1}^n a_{ij} k_j u_j}{k_i u_i} \leq \lambda_1, \quad i = 1, 2, \dots, n.$$

Solving λ_1 from (4.10) and plugging it into (4.12), (4.12) is equivalent to

$$(4.13) \quad a_{ii} \rho' k_i u_i \leq \sum_{j \neq i} a_{ij} u_j (\rho k_i - (\rho + \rho') k_j) \quad \forall i = 1, 2, \dots, n.$$

Since $|a_{ii}| \geq \sum_{j \neq i} a_{ij}$ as $-A^T$ is sub-Laplacian, (4.13) holds if

$$\rho' k_i u_i \geq u_j ((\rho + \rho') k_j - \rho k_i) \quad \forall j \neq i,$$

which is equivalent to

$$(4.14) \quad \frac{k_i}{k_j} \geq \frac{u_j (\rho + \rho')}{\rho' u_i + \rho u_j} \quad \forall j \neq i.$$

By Lemma 4.1, we can find k_i satisfying (4.14) (if $u_i = u_j$, we may set $k_i = k_j$). This proves $s(A_{\rho+\rho'}) \leq s(A_\rho)$.

If $-A^T$ is strongly sub-Laplacian, then the inequality (4.12) is strict and $s(A_\rho)$ is strictly decreasing. $\square$

Next, we show that $s(\rho A + Q)$ is analytic in ρ . Since the zeros of analytic functions are isolated and $s(\rho A + Q)$ is decreasing, $s(\rho A + Q)$ is either strictly decreasing or constant in ρ .

LEMMA 4.3. *Let $A = (a_{ij})_{n \times n}$ be an irreducible essentially nonnegative matrix such that $-A^T$ is sub-Laplacian, and let $Q = \text{diag}(q_i)$ be a real diagonal matrix. Then $s(\rho A + Q)$ is either strictly decreasing or constant in $\rho \in (0, \infty)$.*

Proof. By the Perron–Frobenius theorem, $s^*(\rho) := s(\rho A + Q)$ is a simple root of some polynomial equation $F(\rho, s) = 0$ for each $\rho \in (0, \infty)$. Therefore,

$$\frac{\partial F}{\partial s}(\rho, s^*) \neq 0 \quad \forall \rho \in (0, \infty).$$

By the implicit function theorem, $s^*(\rho)$ is analytic in ρ (we may extend the domain of ρ and s to the complex plane). Since the zeros of analytic functions are isolated and $s(\rho A + Q)$ is decreasing by Lemma 4.2, $s(\rho A + Q)$ is either strictly decreasing or constant in ρ . $\square$

Now we are ready to establish monotonicity of the spectral bound $s(\rho A + Q)$.

THEOREM 4.4. *Let $A = (a_{ij})_{n \times n}$ be an irreducible essentially nonnegative matrix and let $Q = \text{diag}(q_i)$ be a real diagonal matrix. Then the following results hold:*

1. *If $s(A) < 0$, then $s(\rho A + Q)$ is strictly decreasing in $\rho \in (0, \infty)$. Moreover*

$$\lim_{\rho \rightarrow 0} s(\rho A + Q) = \max_{1 \leq i \leq n} \{q_i\} \quad \text{and} \quad \lim_{\rho \rightarrow \infty} s(\rho A + Q) = -\infty.$$

2. If $s(A) = 0$, then $s(\rho A + Q)$ is strictly decreasing provided that Q is not a multiple of I . Moreover,

$$\lim_{\rho \rightarrow 0} s(\rho A + Q) = \max_{1 \leq i \leq n} \{q_i\} \quad \text{and} \quad \lim_{\rho \rightarrow \infty} s(\rho A + Q) = \sum_{i=1}^n v_i q_i,$$

where $v_i \in (0, 1)$ for each $1 \leq i \leq n$ is determined by A and satisfies $\sum_{i=1}^n v_i = 1$ (if A has each row sum equaling zero, then v is a left positive eigenvector of A).

Proof. It is easy to see that $\lim_{\rho \rightarrow 0} s(\rho A + Q) = \max_{1 \leq i \leq n} \{q_i\}$. Let $u = (u_1, u_2, \dots, u_n)^T$ be the positive eigenvector of A corresponding to $s(A)$ satisfying $\sum_{i=1}^n u_i = 1$ and let $U = \text{diag}(u_i)$. Let $\tilde{A} := U^{-1}AU = (u_i^{-1}a_{ij}u_j)$. Then the sum of the i th row of $\tilde{A}$ is

$$(4.15) \quad u_i^{-1} \sum_{j=1}^n a_{ij}u_j = u_i^{-1}s(A)u_i = s(A).$$

If $s(A) < 0$, then $\tilde{A}$ is essentially nonnegative, and $-\tilde{A}^T$ is strongly sub-Laplacian by (4.15). By Lemma 4.2, $s(\rho A + Q) = s(\rho \tilde{A} + Q)$ is strictly decreasing. Since

$$(4.16) \quad \min_{1 \leq i \leq n} \left\{ \rho \sum_{j=1}^n a_{ij} + q_i \right\} \leq s(\rho A + Q) \leq \max_{1 \leq i \leq n} \left\{ \rho \sum_{j=1}^n a_{ij} + q_i \right\},$$

and $\sum_{j=1}^n a_{ij} < 0$ for each i , we have $\lim_{\rho \rightarrow \infty} s(\rho A + Q) = -\infty$.

If $s(A) = 0$, then $\tilde{A}$ is essentially nonnegative and $-\tilde{A}^T$ is Laplacian by (4.15). By Lemma 4.3, $s(\rho A + Q) = s(\rho \tilde{A} + Q)$ is strictly decreasing or constant in ρ . By (4.16), $s(\rho \tilde{A} + Q)$ is bounded below by $\min_{1 \leq i \leq n} \{q_i\}$ and above by $\max_{1 \leq i \leq n} \{q_i\}$. Therefore, $\lim_{\rho \rightarrow \infty} s(\rho \tilde{A} + Q)$ exists. Let $v_\rho = (v_{\rho 1}, v_{\rho 2}, \dots, v_{\rho n})$ be the left positive satisfying $\sum_{i=1}^n v_{\rho i} = 1$ for $\rho \tilde{A} + Q$. Up to a subsequence, we have $v_\rho \rightarrow v = (v_1, v_2, \dots, v_n)$ as $\rho \rightarrow \infty$ for some nonnegative vector v satisfying $\sum_{i=1}^n v_i = 1$. Dividing $v_\rho(\rho \tilde{A} + Q) = s(\rho A + Q) = s(\rho \tilde{A} + Q)v_\rho$ by ρ and taking $\rho \rightarrow \infty$, we obtain $v\tilde{A} = 0$. Therefore, v is the left positive $\tilde{A}$ satisfying $\sum_{i=1}^n v_i = 1$. Summing up all the equations of $v_\rho(\rho \tilde{A} + Q) = s(\rho \tilde{A} + Q)v_\rho$ and using the fact that $\tilde{A}$ has each row sum equaling zero, we obtain

$$\sum_{i=1}^n v_{\rho i} q_i = s(\rho \tilde{A} + Q) \sum_{i=1}^n v_i = s(\rho \tilde{A} + Q).$$

Taking $\rho \rightarrow \infty$, we have

$$\lim_{\rho \rightarrow \infty} s(\rho \tilde{A} + Q) = \sum_{i=1}^n v_i q_i.$$

Since $\sum_{i=1}^n v_i q_i < \max_{1 \leq i \leq n} \{q_i\}$ if and only if $(q_1, q_2, \dots, q_n)$ is not a multiple of $(1, 1, \dots, 1)$, $s(\rho \tilde{A} + Q)$ is strictly decreasing if Q is not a multiple of I . $\square$

5. Applications. In this section we apply Theorem 1.1 (also Theorem 4.4) to several metapopulation models in the literature of spatial biology.

5.1. Single species model. We consider a general single species model in a heterogeneous environment of n patches ($n \geq 2$),

$$(5.1) \quad u'_i = u_i f_i(u_i) + \rho \sum_{j=1}^n (a_{ij} u_j - a_{ji} u_i) - \rho \epsilon_i u_i, \quad i = 1, \dots, n,$$

where u_i denotes the population size (or density) in patch i ; function f_i denotes the intrinsic growth rate in patch i ; the connectivity matrix $A = (a_{ij})_{n \times n}$ describes the dispersal pattern between patches, where $a_{ij} \geq 0$ for $i \neq j$ quantifies the dispersal from patch j to patch i , and $a_{jj} = -\sum_{i \neq j} a_{ij}$ is the total movement out from patch j ; $\rho \geq 0$ is the dispersal rate; and $\epsilon_i \geq 0$ is the death rate due to dispersal. When $\epsilon_i = 0$ for all i , there is no loss of individuals during the movement between patches; and when $\epsilon_i > 0$ for some $1 \leq i \leq n$, there are losses of individuals during the movement between patches. The intrinsic growth function f_i ($1 \leq i \leq n$) satisfies the following:

- (f) For $1 \leq i \leq n$, $f_i : \mathbb{R}_+ \rightarrow \mathbb{R}$ is continuous and strictly decreasing. Moreover, there exists $c_i > 0$ such that $f_i(u_i) < 0$ for all $u_i > c_i$.

System (5.1) admits a trivial equilibrium $E_0 = (0, 0, \dots, 0)$, representing the state of species extinction, and its stability can be determined by the Jacobian matrix $J = \rho(A - \text{diag}(\epsilon_i)) + \text{diag}(f_i(0))$.

Assume that A is irreducible. It follows from the Perron–Frobenius theorem that $A - \text{diag}(\epsilon_i)$ has a principal eigenvector $(\alpha_1, \alpha_2, \dots, \alpha_n)^T > 0$ corresponding to the principal eigenvalue 0 such that $\alpha_i > 0$ for all i . As shown in Theorem 4.4, α_i serves as the weight constant in determining the impact of patch i on the dynamics of the interconnected system (5.1) for larger value of ρ . The following result describes this phenomenon in detail.

THEOREM 5.1. *Suppose that A is an irreducible essentially nonnegative matrix, and assume (f) is satisfied. Let $(\alpha_1, \alpha_2, \dots, \alpha_n)^T > 0$ denote the normalized eigenvector of $A - \text{diag}(\epsilon_i)$ corresponding to the principal eigenvalue 0 such that $\sum_{i=1}^n \alpha_i = 1$. Let $M = \max_{1 \leq i \leq n} \{f_i(0)\}$ and $m = \sum_{i=1}^n \alpha_i f_i(0)$. Then the following statements hold:*

- (i) *If $M < 0$, then the equilibrium E_0 is globally asymptotically stable in $\mathbb{R}_+^n$ for all $\rho > 0$.*
- (ii) *If $\epsilon_i = 0$ for all $1 \leq i \leq n$ and $m > 0$, then the equilibrium E_0 is unstable for all $\rho > 0$. Furthermore, system (5.1) admits a unique positive equilibrium $E^* = (u_1^*, \dots, u_n^*)$, which is globally asymptotically stable in $\mathbb{R}_+^n - \{E_0\}$.*
- (iii) *If either $\epsilon_i = 0$ for all $1 \leq i \leq n$ and $m < 0 < M$, or $\epsilon_i > 0$ for at least some $i \in \{1, \dots, n\}$ and $M > 0$, then there exists a unique $\rho^* > 0$ such that E_0 is globally asymptotically stable in $\mathbb{R}_+^n$ for $\rho \geq \rho^*$ while E_0 is unstable for $0 < \rho < \rho^*$. Furthermore, if $0 < \rho < \rho^*$, then there exists a unique positive equilibrium E^* , which is globally asymptotically stable in $\mathbb{R}_+^n - \{E_0\}$.*

Proof. The local stability of E_0 is determined by the sign of the spectral bound of the Jacobian matrix $J(\rho) = \rho(A - \text{diag}(\epsilon_i)) + \text{diag}(f_i(0))$, i.e., E_0 is locally asymptotically stable if $s(J(\rho)) < 0$ and it is unstable if $s(J(\rho)) > 0$. By Theorem 4.4, if $\epsilon_i = 0$ for all $1 \leq i \leq n$, $s(J(\rho))$ is nonincreasing for $\rho \in (0, \infty)$ with

$$m = \lim_{\rho \rightarrow \infty} s(J(\rho)) \leq s(J(\rho)) \leq \lim_{\rho \rightarrow 0} s(J(\rho)) = M,$$

and if $m < M$, then $s(J(\rho))$ is strictly decreasing; if $\epsilon_i > 0$ for at least some $i \in \{1, \dots, n\}$, $s(J(\rho))$ is strictly decreasing in ρ with

$$-\infty = \lim_{\rho \rightarrow \infty} s(J(\rho)) < s(J(\rho)) < \lim_{\rho \rightarrow 0} s(J(\rho)) = M.$$

The claim on the local stability of E_0 follows from these observations.

Since A is irreducible and essentially nonnegative, (5.1) generates a strongly monotone dynamical system [38]. Since f_i is strictly decreasing for $1 \leq i \leq n$, the semiflow generated by (5.1) is strongly subhomogeneous [42] (i.e., $\lambda T(t)u_0 \ll T(t)\lambda u_0$ for all $\lambda \in (0, 1)$ and initial data $u_0 \gg 0$, where $T(t)$ is the semiflow induced by (5.1)). Moreover, by the assumption (f), the solutions of (5.1) are bounded and dissipative (i.e., uniformly ultimately bounded). Therefore, by [42, Theorem 2.3.4], if $s(J(\rho)) \leq 0$, E_0 is globally stable; if $s(J(\rho)) > 0$, E_0 is unstable and there exists a unique globally stable positive steady state E^* . This completes the proof. $\square$

Remark 5.2. 1. If the maximum growth rates $f_i(0)$ at the i th patch are not all identical, then $m < M$.

- 2 The i th patch is a sink if $f_i(0) \leq 0$ and it is a source if $f_i(0) > 0$. If all patches are source, then apparently $m > 0$, but the population can still become extinct for large ρ if there is population loss during dispersal. If some patches are sink, then it is possible that $m < 0$ but it still depends on the network connection. When the sink patches carries a larger weight α_i , it is more likely that $m < 0$. This extends earlier results on source-sink dynamics with symmetric movement [21].
3. The extinction/persistence dichotomy of dynamics in terms of stability of extinction state and the global stability of positive equilibrium of (5.1) are well-known; see, for example, [10, 30, 32]. Theorem 5.1 shows how the extinction or persistence of population depends on the dispersal coefficient ρ .
4. A similar result for reducible A can also be obtained by using Corollary 3.3 and the approach in [14].

5.2. Predator-prey model. We consider the following predator-prey model with a general functional response in heterogeneous environment of n patches ($n \geq 2$):

$$(5.2) \quad \begin{cases} u'_i = r_i u_i \left(1 - \frac{u_i}{K_i}\right) - g_i(u_i)v_i + \rho_u \sum_{j=1}^n (a_{ij}u_j - a_{ji}u_i), & i = 1, 2, \dots, n, \\ v'_i = v_i(c_i g_i(u_i) - d_i) + \rho_v \sum_{j=1}^n (b_{ij}v_j - b_{ji}v_i), & i = 1, 2, \dots, n, \end{cases}$$

where u_i and v_i denote the population density of the prey and the predators in the i th patch, respectively; $r_i, K_i > 0$ are the growth rate and carrying capacity of the prey in the i th patch, respectively; d_i is the mortality rate of the predator, and c_i is the conversion rate of the predation; the connectivity matrices $A = (a_{ij})_{n \times n}$ and $B = (b_{ij})_{n \times n}$ describe the dispersal pattern between patches for prey and predators respectively, where $a_{ij} \geq 0$ and $b_{ij} \geq 0$, $i \neq j$, denote rate of the prey and predators from patch j to patch i , and $a_{jj} = -\sum_{i \neq j} a_{ij}$ and $b_{jj} = -\sum_{i \neq j} b_{ij}$ are the total movement out from patch j of the prey and predators, respectively; and $\rho_u, \rho_v \geq 0$ denote the rates of dispersal of the two species u and v , respectively. Function g_i denotes the functional response of predator in the i th patch and satisfies the following assumption.

- (g) For $1 \leq i \leq n$, $g_i : \mathbb{R}_+ \rightarrow \mathbb{R}_+$ is continuous and strictly increasing and $g_i(0) = 0$.

The following result highlights the impact of dispersal rates on population dynamics of (5.2).

THEOREM 5.3. Suppose that A and B are irreducible matrices, and assume (g) is satisfied. Let $(\alpha_1, \alpha_2, \dots, \alpha_n)^T$ be the positive eigenvector of B corresponding to eigenvalue 0 with $\sum_{i=1}^n \alpha_i = 1$. Then for any $\rho_u > 0$, $\rho_v > 0$, system (5.2) admits a trivial equilibrium $E_0 = (0, 0, \dots, 0)$ and a unique semitrivial equilibrium $E_1 = (u_1^*, \dots, u_n^*, 0, \dots, 0)$, where $u_i^* > 0$ and satisfies

$$(5.3) \quad r_i u_i^* \left(1 - \frac{u_i^*}{K_i}\right) + \rho_u \sum_{j=1}^n (a_{ij} u_j^* - a_{ji} u_i^*) = 0, \quad j = 1, 2, \dots, n.$$

Denote $M = \max_{1 \leq i \leq n} \{c_i g_i(u_i^*) - d_i\}$ and $m = \sum_{i=1}^n \alpha_i (c_i g_i(u_i^*) - d_i)$. Then the following statements hold:

- (i) E_0 is unstable for any $\rho_v > 0$.
- (ii) If $M < 0$, then the equilibrium E_1 is globally asymptotically stable in $\mathbb{R}_+^{2n} - \{E_0\}$ for all $\rho_v > 0$.
- (iii) If $m > 0$, then the equilibrium E_1 is unstable for all $\rho_v > 0$.
- (iv) If $m < 0 < M$, then there exists a unique $\rho_v^* > 0$ such that E_1 is globally asymptotically stable in $\mathbb{R}_+^{2n} - \{E_0\}$ for $\rho_v > \rho_v^*$ while E_1 is unstable for $0 < \rho_v < \rho_v^*$.

Proof. The existence and uniqueness of E_1 follow from Theorem 5.1. We prove the local stability/instability of E_1 in (ii)–(iv), as the proof of (i) is similar and simpler. Linearizing (5.2) at E_1 , the local stability of E_1 is determined by the following eigenvalue problem:

$$(5.4) \quad \begin{cases} \lambda \phi_i = r_i \phi_i \left(1 - 2 \frac{u_i^*}{K_i}\right) - g(u_i^*) \psi_i + \rho_u \sum_{j=1}^n (a_{ij} \phi_j - a_{ji} \phi_i), & i = 1, 2, \dots, n, \\ \lambda \psi_i = \psi_i (c_i g(u_i^*) - d_i) + \rho_v \sum_{j=1}^n (a_{ij} \psi_j - a_{ji} \psi_i), & i = 1, 2, \dots, n. \end{cases}$$

If $\operatorname{Re} \lambda < 0$ for any eigenvalue λ of (5.4), then E_1 is locally asymptotically stable; if (5.4) has an eigenvalue λ with $\operatorname{Re} \lambda > 0$, then E_1 is unstable.

We claim that the local stability of E_1 is determined by the sign of $s(\rho_v A + \operatorname{diag}(c_i g_i(u_i^*) - d_i))$. To see this, let (ϕ, ψ) with $\phi = (\phi_1, \phi_2, \dots, \phi_n)^T$ and $\psi = (\psi_1, \psi_2, \dots, \psi_n)^T$ be an eigenvector of (5.4) corresponding to eigenvalue λ . If $\psi = 0$, then λ is an eigenvalue of

$$\lambda \phi_i = r_i \phi_i \left(1 - 2 \frac{u_i^*}{K_i}\right) + \rho_u \sum_{j=1}^n (a_{ij} \phi_j - a_{ji} \phi_i), \quad i = 1, \dots, n,$$

i.e., an eigenvalue of $\rho_u A + \operatorname{diag}(r_i(1 - 2u_i^*/K))$. By (5.3) and the Perron–Frobenius theorem, $s(\rho_u A + \operatorname{diag}(r_i(1 - 2u_i^*/K))) = 0$. Therefore, $s(\rho_u A + \operatorname{diag}(r_i(1 - 2u_i^*/K))) < s(\rho_u A + \operatorname{diag}(r_i(1 - u_i^*/K))) = 0$. Hence, we have

$$(5.5) \quad \operatorname{Re} \lambda \leq s(\rho_u A + \operatorname{diag}(r_i(1 - 2u_i^*/K))) < 0.$$

If $\psi \neq 0$, λ is an eigenvalue of

$$\lambda \psi_i = \psi_i (c_i g(u_i^*) - d_i) + \rho_v \sum_{j=1}^n (a_{ij} \psi_j - a_{ji} \psi_i), \quad i = 1, \dots, n,$$

i.e., λ is an eigenvalue of $\rho_v A + \operatorname{diag}(c_i g_i(u_i^*) - d_i)$. Noticing (5.5), we see that the local stability of E_1 is determined by the sign of $s(\rho_v A + \operatorname{diag}(c_i g_i(u_i^*) - d_i))$. Then the results (ii)–(iv) on the local stability of E_1 follow from the claim and Theorems 1.1 and 4.4.

It remains to prove the global stability of E_1 when $s(\rho_v A + \operatorname{diag}(c_i g_i(u_i^*) - d_i)) < 0$. Suppose that $(u_1(0), \dots, u_n(0))$ is nontrivial. Let $\hat{u}_i(t)$, $1 \leq i \leq n$, be the solution of

$$\begin{cases} \hat{u}'_i = r_i \hat{u}_i \left(1 - \frac{\hat{u}_i}{K_i}\right) + \rho_u \sum_{j=1}^n (a_{ij} \hat{u}_j - a_{ji} \hat{u}_i), & i = 1, 2, \dots, n, \\ \hat{u}_i(0) = u_i(0), & i = 1, 2, \dots, n. \end{cases}$$

By the comparison principle, we have $u_i(t) \leq \hat{u}_i(t)$ for all $t \geq 0$ and $1 \leq i \leq n$. By Theorem 5.1, we have $\lim_{t \rightarrow \infty} \hat{u}_i(t) = u_i^*$, and it follows that $\limsup_{t \rightarrow \infty} \hat{u}_i(t) = u_i^*$ for $1 \leq i \leq n$. Choose $\epsilon_0 > 0$ such that $s(\rho_v A + \text{diag}(c_i g_i(u_i^* + \epsilon_0) - d_i)) < 0$. Then there exists $T > 0$ such that $u_i(t) \leq u_i^* + \epsilon_0$ for all $t \geq T$. By the second equation of (5.2) and the monotonicity of g_i , we have

$$\begin{cases} v'_i \leq v_i(c_i g(u_i^* + \epsilon_0) - d_i) + \rho_v \sum_{j=1}^n (b_{ij} v_j - b_{ji} v_i), & t \geq T, i = 1, 2, \dots, n, \\ v_i(T) \leq C \tilde{\alpha}_i, & t \geq T, i = 1, 2, \dots, n, \end{cases}$$

where $(\tilde{\alpha}_1, \tilde{\alpha}_2, \dots, \tilde{\alpha}_n)$ is a positive principal eigenvector of $\rho_v A + \text{diag}(c_i g_i(u_i^* + \epsilon_0) - d_i)$ corresponding with eigenvalue $s_0 := s(\rho_v A + \text{diag}(c_i g_i(u_i^* + \epsilon_0) - d_i))$ and $C > 0$ is large. By the comparison principle, we have $v_i(t) \leq \hat{v}_i(t)$ for $t \geq T$, where $\hat{v}_i$ is the solution of the problem

$$(5.6) \quad \begin{cases} \hat{v}'_i = \hat{v}_i(c_i g(u_i^* + \epsilon_0) - d_i) + \rho_v \sum_{j=1}^n (b_{ij} \hat{v}_j - b_{ji} \hat{v}_i), & t \geq T, i = 1, 2, \dots, n, \\ \hat{v}_i(T) = C \tilde{\alpha}_i, & t \geq T, i = 1, 2, \dots, n. \end{cases}$$

It is easy to check that the solution of (5.6) is $\hat{v}_i(t) = C \tilde{\alpha}_i e^{s_0(t-T)}$, $1 \leq i \leq n$. Since $s_0 < 0$, we have $\lim_{t \rightarrow \infty} \hat{v}_i(t) = 0$, which implies $\lim_{t \rightarrow \infty} v_i(t) = 0$. Finally by the theory of asymptotically autonomous semiflows (see, e.g., [41]) and Theorem 5.1, we have $\lim_{t \rightarrow \infty} u_i(t) = u_i^*$, $1 \leq i \leq n$. $\square$

- Remark 5.4.* 1. When $\rho_v = 0$, then $s(\rho_v A + \text{diag}(c_i g_i(u_i^*) - d_i)) = M$ so part (ii) in Theorem 5.3 still holds.
2. When E_1 is unstable, one can show the existence of a coexistence equilibrium E_2 through the theory of uniform persistence. When the functional response g_i is of Lotka–Volterra type ($g_i(u_i) = u_i$), E_2 can be shown to be globally asymptotically stable when $\rho_v = 0$ (see [30, Theorem 6.1]). But when g_i is of Monod type ($g_i(u_i) = u_i/(a_i + u_i)$), (5.2) is an n -patch Rosenzweig–MacArthur predator–prey system, E_2 may be unstable, and the system could have a limit cycle even in the one-patch case.
3. In Theorem 5.3, the growth rate r_i for the prey is assumed to be positive in all patches. If r_i are not all positive, then from Theorem 5.1, a unique critical prey dispersal rate $\rho_u^* > 0$ may exist so that E_0 is globally asymptotically stable for $\rho_u > \rho_u^*$ while E_0 is unstable for $0 < \rho_u < \rho_u^*$. In that case, results (ii)–(iv) in Theorem 5.3 hold for $0 < \rho_u < \rho_u^*$.

5.3. Lotka–Volterra competition model. We consider the following Lotka–Volterra competition model in a heterogeneous environment of n patches ($n \geq 2$):

$$(5.7) \quad \begin{cases} u'_i = u_i(p_i - u_i - v_i) + \rho_u \sum_{j=1}^n (a_{ij} u_j - a_{ji} u_i), & i = 1, \dots, n, \\ v'_i = v_i(p_i - u_i - v_i) + \rho_v \sum_{j=1}^n (a_{ij} v_j - a_{ji} v_i), & i = 1, \dots, n, \\ u(0) = u_0 \geq (\neq) 0, v(0) = v_0 \geq (\neq) 0, \end{cases}$$

where $u = (u_1, \dots, u_n)$ and $v = (v_1, \dots, v_n)$, and u_i and v_i denote the population densities of two competing species in patch i , respectively; $\rho_u, \rho_v \geq 0$ are the dispersal rates of the two species, respectively; $p_i \in \mathbb{R}$ represents the intrinsic growth rates of species u_i and v_i in patch i ; and $a_{ij} \geq 0$ ($i \neq j$) is the movement rate from patch j to patch i , $a_{jj} = -\sum_{i \neq j} a_{ij}$ is the total movement out from patch j , and the matrix $A = (a_{ij})$ is irreducible. Let $(\alpha_1, \alpha_2, \dots, \alpha_n)^T$ be the positive eigenvector of A satisfying $\sum_{i=1}^n \alpha_i = 1$. The two competing species are assumed to be identical except for the dispersal rates.

Denote $M = \max_{1 \leq i \leq n} \{p_i\}$ and $m = \sum_{i=1}^n \alpha_i p_i$. If $M < 0$, then the trivial equilibrium is the only nonnegative equilibrium, which is globally asymptotically stable. Therefore, in the following we assume that $M > 0$. By Theorem 5.1, we obtain the following result about the existence/nonexistence of nonnegative semitrivial equilibria.

LEMMA 5.5. *Suppose $M > 0$ and $\rho_u < \rho_v$. Then the following results hold:*

- (i) *If $m > 0$, then system (5.7) admits exactly two nonnegative semitrivial equilibria $(u^*, 0)$ and $(0, v^*)$, where $w^* = (w_1^*, \dots, w_n^*)$ for $w = u, v$.*
- (ii) *If $m < 0$, then there exists a unique $\rho_* > 0$ such that $s(\rho_* A + \text{diag}(p_i)) = 0$. Moreover, when $\rho_* \leq \rho_u < \rho_v$, there exists no nonnegative semitrivial equilibrium; when $\rho_u < \rho_* \leq \rho_v$, there exists exactly one nonnegative semitrivial equilibrium $(u^*, 0)$; and when $\rho_u < \rho_v < \rho_*$, there exist exactly two nonnegative semitrivial equilibria $(u^*, 0)$ and $(0, v^*)$.*

Next we show that system (5.7) has no positive equilibrium.

LEMMA 5.6. *Suppose $M > 0$ and $\rho_u < \rho_v$. If $(p_1, p_2, \dots, p_n)$ is not a multiple of $(\alpha_1, \alpha_2, \dots, \alpha_n)$, then system (5.7) admits no nonnegative equilibrium $(\bar{u}, \bar{v}) = (\bar{u}_1, \dots, \bar{u}_n, \bar{v}_1, \dots, \bar{v}_n)$ with $\bar{u} \geq (\neq) 0$ and $\bar{v} \geq (\neq) 0$.*

Proof. Assume to the contrary that such an equilibrium $(\bar{u}, \bar{v}) = (\bar{u}_1, \dots, \bar{u}_n, \bar{v}_1, \dots, \bar{v}_n)$ exists. Let $Q = \text{diag}(p_i - \bar{u}_i - \bar{v}_i)$. Since $(\bar{u}, \bar{v})$ is an equilibrium of (5.7), we have

$$\begin{aligned} \bar{u}_i(p_i - \bar{u}_i - \bar{v}_i) + \rho_u \sum_{j=1}^n a_{ij} \bar{u}_j &= 0, \quad i = 1, 2, \dots, n, \\ \bar{v}_i(p_i - \bar{u}_i - \bar{v}_i) + \rho_v \sum_{j=1}^n a_{ij} \bar{v}_j &= 0, \quad i = 1, 2, \dots, n. \end{aligned}$$

Therefore, $\bar{u}$ and $\bar{v}$ are nonnegative eigenvectors of $\rho_u A + Q$ and $\rho_v A + Q$ corresponding with eigenvalue 0, respectively. Since A is irreducible, by the Perron–Frobenius theorem, we have

$$s(\rho_u A + Q) = s(\rho_v A + Q) = 0.$$

Since $\rho_u < \rho_v$, by Theorem 1.1 or Theorem 4.4, Q is a multiple of I and $\bar{u}, \bar{v}$ are eigenvectors of A . It follows that $p_1 - u_1 - v_1 = p_2 - u_2 - v_2 = \dots = p_n - u_n - v_n = 0$ and $(p_1, p_2, \dots, p_n)$ is a multiple of $(\alpha_1, \alpha_2, \dots, \alpha_n)$, which is a contradiction. This completes the proof. $\square$

In the following, we will use monotone dynamical system theory [24, 38] to investigate the global dynamics of (5.7). Let $\leq_K, <_K, \ll_K$ be the order of $\mathbb{R}^n \times \mathbb{R}^n$ generated by the cone $\mathbb{R}_+^n \times (-\mathbb{R}_+^n)$ defined in the usual way. For example, $(u, v) <_K (w, z)$ means

$$u \leq w, \quad v \geq z \quad \text{and} \quad (u, v) \neq (w, z).$$

Then the solutions of system (5.7) induce a strictly monotone semiflow on $\mathbb{R}_+^n \times \mathbb{R}_+^n$.

LEMMA 5.7. Let $(u^{(i)}(t), v^{(i)}(t))$ be the corresponding solutions of (5.7) with non-negative initial value $(u_0^{(i)}, v_0^{(i)})$ for $i = 1, 2$, where $u_0^{(2)} \geq (\neq) 0$, $v_0^{(1)} \geq (\neq) 0$ and

$$(u_0^{(2)}, v_0^{(2)}) <_K (u_0^{(1)}, v_0^{(1)}).$$

Then $(u^{(2)}(t), v^{(2)}(t)) \ll_K (u^{(1)}(t), v^{(1)}(t))$ for any $t > 0$.

Proof. Since $u^{(2)}(t)$ is the solution of

$$\begin{cases} u'_i = u_i(p_i - u_i - v_i) + \rho_u \sum_{j=1}^n (a_{ij}u_j - a_{ji}u_i), & i = 1, 2, \dots, n, \\ u(0) = u_0^{(2)} \geq (\neq) 0, \end{cases}$$

and A is essentially nonnegative and irreducible, we have $u^{(2)}(t) \gg 0$ for all $t > 0$ (see [38]). Similarly, $v^{(1)}(t) \gg 0$ for all $t > 0$.

Let $\bar{u}(t) = u^{(1)}(t) - u^{(2)}(t)$, $\bar{v}(t) = v^{(2)}(t) - v^{(1)}(t)$, $\bar{u}_0 = u_0^{(1)} - u_0^{(2)}$, and $\bar{v}_0 = v_0^{(2)} - v_0^{(1)}$. Then $(\bar{u}(t), \bar{v}(t))$ satisfies

$$(5.8) \quad \begin{cases} \bar{u}_i = \rho_u \sum_{j=1}^n a_{ij}\bar{u}_j + \bar{u}_i(p_i - u_i^{(1)} - u_i^{(2)} - v_i^{(1)}) + u_i^{(2)}\bar{v}_i, \\ \bar{v}_i = \rho_v \sum_{j=1}^n a_{ij}\bar{v}_j + \bar{v}_i(p_i - v_i^{(1)} - v_i^{(2)} - u_i^{(2)}) + v_i^{(1)}\bar{u}_i, \\ (\bar{u}(0), \bar{v}(0)) \geq (\neq) 0. \end{cases}$$

Since $u_i^{(2)}, v_i^{(1)} > 0$ for all $t > 0$, $i = 1, 2, \dots, n$, and A is essentially nonnegative and irreducible, (5.8) is cooperative and irreducible [38]. It then follows that $\bar{u}_i(t), \bar{v}_i(t) > 0$ for any $i = 1, 2, \dots, n$ and $t > 0$. This proves the claim. $\square$

Since the solutions of system (5.7) induce a strictly monotone semiflow on $\mathbb{R}_+^n \times \mathbb{R}_+^n$, we can use the theory of monotone dynamical systems in [23, 24, 28, 38] to investigate the asymptotic behavior of (5.7). Specifically, if $(u^*, 0)$ is the only semitrivial equilibrium which is locally asymptotically stable, then it is globally asymptotically stable; if both $(u^*, 0)$ and $(0, v^*)$ exist with $(u^*, 0)$ stable and $(0, v^*)$ unstable and there exists no positive equilibrium, then $(u^*, 0)$ is globally asymptotically stable. Then the following result follows from Lemmas 5.5–5.6.

THEOREM 5.8. Suppose that $M > 0$, $\rho_u < \rho_v$, and $(p_1, p_2, \dots, p_n)$ is not a multiple of $(\alpha_1, \alpha_2, \dots, \alpha_n)$. Let ρ_* , u^* be defined as in Lemma 5.5. Then the following statements hold:

- (i) If $m > 0$, then semitrivial equilibrium $(u^*, 0)$ is globally asymptotically stable.
- (ii) If $m < 0$, then the trivial equilibrium is globally asymptotically stable for $\rho_u \geq \rho_*$, and the semitrivial $(u^*, 0)$ is globally asymptotically stable for $\rho_u < \rho_*$.

Proof. By Lemma 5.5, $(u^*, 0)$ always exists. We show that $(u^*, 0)$ is locally asymptotically stable whenever it exists. Linearizing (5.7) at $(u^*, 0)$, we obtain the following eigenvalue problem:

$$(5.9) \quad \begin{cases} \lambda\phi_i = \phi_i(p_i - 2u_i^*) - u_i^*\psi_i + \rho_u \sum_{j=1}^n (a_{ij}\phi_j - a_{ji}\phi_i), & i = 1, 2, \dots, n, \\ \lambda\psi_i = \psi_i(p_i - u_i^*) + \rho_v \sum_{j=1}^n (a_{ij}\psi_j - a_{ji}\psi_i), & i = 1, 2, \dots, n. \end{cases}$$

It suffices to show $\operatorname{Re} \lambda < 0$ for any eigenvalue λ of (5.9). Let (ϕ, ψ) with $\phi = (\phi_1, \phi_2, \dots, \phi_n)$ and $\psi = (\psi_1, \psi_2, \dots, \psi_n)$ be an eigenvector corresponding to λ . If $\psi = 0$, then λ satisfies

$$\lambda \phi_i = \phi_i(p_i - 2u_i^*) + \rho_u \sum_{j=1}^n (a_{ij} \phi_j - a_{ji} \phi_i), \quad i = 1, 2, \dots, n,$$

namely, λ is an eigenvalue of $\rho_u A + \operatorname{diag}(p_i - 2u_i^*)$. Since A is essentially nonnegative and irreducible and u^* satisfies

$$0 = u_i^*(p_i - u_i^*) + \rho_u \sum_{j=1}^n (a_{ij} u_j^* - a_{ji} u_i^*), \quad i = 1, 2, \dots, n,$$

u^* is a positive eigenvector of $\rho_u A + \operatorname{diag}(p_i - u_i^*)$ corresponding with principal eigenvalue $s(\rho_u A + \operatorname{diag}(p_i - u_i^*)) = 0$. Therefore, $s(\rho_u A + \operatorname{diag}(p_i - 2u_i^*)) < s(\rho_u A + \operatorname{diag}(p_i - u_i^*)) = 0$. It follows that

$$\operatorname{Re} \lambda \leq s(\rho_u A + \operatorname{diag}(p_i - 2u_i^*)) < 0.$$

Therefore, we may assume $\psi \neq 0$. Then, λ satisfies

$$\lambda \psi_i = \psi_i(p_i - u_i^*) + \rho_v \sum_{j=1}^n (a_{ij} \psi_j - a_{ji} \psi_i), \quad i = 1, 2, \dots, n,$$

i.e., λ is an eigenvalue of $\rho_v A + \operatorname{diag}(p_i - u_i^*)$. Since $s(\rho_u A + \operatorname{diag}(p_i - u_i^*)) = 0$ and $\rho_u < \rho_v$, $s(\rho_v A + \operatorname{diag}(p_i - u_i^*)) < 0$ by Theorems 1.1 or 4.4. Hence, $\operatorname{Re} \lambda < 0$. This implies that $(u^*, 0)$ is locally asymptotically stable. Similarly, we have $s(\rho_v A + \operatorname{diag}(p_i - v_i^*)) > 0$ and $(0, v^*)$ is unstable if it exists. By Lemma 5.6, (5.7) has no positive equilibrium. Therefore, the results follow from the theory of strictly monotone dynamical systems [23, 24, 28, 38, 39]. $\square$

- Remark 5.9.* 1. For the reaction-diffusion Lotka–Volterra competition model, it was shown in [12] that the species with slower diffusion rate outcompetes the one with faster diffusion rate, when the two species are identical except for the diffusion rates. Theorem 5.8 is an analogous result for the patch model.
2. When $p = (p_1, p_2, \dots, p_n)$ is a multiple of $(\alpha_1, \alpha_2, \dots, \alpha_n)$, the nonexistence of positive equilibria in Lemma 5.6 no longer holds. Indeed it is easy to see that for any $s \in [0, 1]$, $((1-s)p, sp)$ is a nonnegative equilibrium of (5.7). The fact that $(p_1, p_2, \dots, p_n)$ is a multiple of $(\alpha_1, \alpha_2, \dots, \alpha_n)$ implies that the movement strategy defined by $A = (a_{ij})$ is an ideal free dispersal strategy with respect to $(p_1, p_2, \dots, p_n)$, and in (5.7), both species have ideal free dispersal strategies with respect to $(p_1, p_2, \dots, p_n)$, hence coexistence can be achieved (see [7]). Theorem 5.8 shows that when neither species takes the ideal free strategy, the slower disperser will prevail.

Appendix A. Notation from graph theory and tree-cycle identity. Let $B = (b_{ij})$ be a nonnegative $n \times n$ matrix. A *weighted digraph* $\mathcal{G} = \mathcal{G}_B$ associated with B can be constructed as follows: $\mathcal{G} = (V, E)$ is a pair of two sets, a set $V = \{1, 2, \dots, n\}$ of vertices and a set E of arcs (i, j) with weight b_{ij} leading from initial vertex j to terminal vertex i . Specifically, $(i, j) \in E(\mathcal{G})$ if and only if $b_{ij} > 0$.

A digraph is *strongly connected* if, for any ordered pair of distinct vertices i, j , there exists a directed path from i to j . A weighted digraph $\mathcal{G}_B$ is strongly connected if and only if the weight matrix B is irreducible [5].

A subdigraph $\mathcal{H}$ of $\mathcal{G}$ is *spanning* if $\mathcal{H}$ and $\mathcal{G}$ have the same vertex set. The *weight* of a subdigraph $\mathcal{H}$ is the product of the weights of all its arcs. A connected subdigraph $\mathcal{T}$ of $\mathcal{G}$ is a *rooted in-tree* if it contains no directed cycle, and there is one vertex, called the root, that is not an initial vertex of any arcs while each of the remaining vertices is an initial vertex of exactly one arc. A subdigraph $\mathcal{Q}$ of $\mathcal{G}$ is *unicyclic* if it is a union of disjoint rooted in-trees whose roots form a directed cycle. Every vertex of unicyclic $\mathcal{Q}$ is an initial vertex of exactly one arc, and thus a unicyclic graph has also been called a functional digraph [20, p. 201].

Notice that our definitions of rooted in-trees and unicyclic graphs (functional digraphs) above are different from those in [30]. Specifically, rooted out-trees and contra-function digraphs (a union of disjoint rooted out-trees whose roots form a directed cycle) are considered in [30], respectively. As a consequence, a slightly different version of tree-cycle identity, analogous to Theorem 2.2 in [30], can be established using Kirchhoff's matrix-tree theorem [34].

THEOREM A.1 (tree-cycle identity). *Let $\mathcal{G}_B$ be a strongly connected weighted digraph. Let $L = (\ell_{ij})$ be the Laplacian matrix of $\mathcal{G}_B$; that is, $\ell_{ij} = -b_{ij}$ for $i \neq j$ and $\ell_{ii} = \sum_{k \neq i} b_{ki}$. Let θ_i be the cofactor of the i th diagonal entry of L for $i = 1, \dots, n$. Then the following identity holds for any $x_i, x_j \in \mathbb{R}^m$, $1 \leq i, j \leq n$, and any family of functions $\{F_{ij} : \mathbb{R}^m \times \mathbb{R}^m \rightarrow \mathbb{R}\}_{1 \leq i, j \leq n}$:*

$$\sum_{i,j=1}^n \theta_i b_{ji} F_{ji}(x_j, x_i) = \sum_{\mathcal{Q} \in \mathbb{Q}} w(\mathcal{Q}) \sum_{(s,r) \in E(\mathcal{C}_{\mathcal{Q}})} F_{sr}(x_s, x_r),$$

where $\mathbb{Q}$ is the set of all spanning unicycle graphs of $(\mathcal{G}_B, B)$, $w(\mathcal{Q}) > 0$ is the weight of $\mathcal{Q}$, and $\mathcal{C}_{\mathcal{Q}}$ denotes the directed cycle of $\mathcal{Q}$ with arc set $E(\mathcal{C}_{\mathcal{Q}})$.

Since $\mathcal{G}_B$ is strongly connected, equivalently, B is irreducible, 0 is a simple eigenvalue of L . Here θ_i is the cofactor of the i th diagonal entry of L and can also be interpreted as $\theta_i = \sum_{\mathcal{T} \in \mathbb{T}_i} w(\mathcal{T})$ where $\mathbb{T}_i$ is the set of all spanning in-trees rooted at i . Therefore, each term in the product $\theta_i b_{ji}$ corresponds to a unicyclic graph that is formed by adding arc (j, i) from i to j to a spanning in-tree rooted at i . So, the same argument as in the proof of [30, Theorem 2.2] can be applied to establish Theorem A.1 and thus is omitted.

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