PERSISTENCE AND GLOBAL ASYMPTOTIC STABILITY
OF SINGLE SPECIES DISPERSAL MODELS
WITH STAGE STRUCTURE

BY

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Abstract. A system of retarded functional differential equations is proposed as a model of single-species population growth with dispersal in a multi-patch environment where individual members of the population have a life history that takes them through two stages, immature and mature. The persistence of the system as well as the existence and global asymptotic stability of a positive equilibrium is proved by using the monotone dynamical systems theory due to Hirsch and Smith, and a convergence theorem established in this paper for nonautonomous retarded equations by using limiting equations theory.

1. Introduction. The effect of environment change in the growth and diffusion of a species in a heterogeneous habitat is a subject of considerable interest in the ecological literature. The theoretical study of this subject was pioneered by Skellam [35] and detailed bibliographies can be found in the work of Levin [29]. To study such a habitat effect, one technique is to divide the habitat into two or more homogeneous patches connected by dispersion. Much research has been devoted to the mathematical analysis of model equations for the growth of single-species population dispersing among patches in a heterogeneous environment. For details we refer to [5, 6, 9–15, 23, 25, 31, 34, 35, 37, 38, 41].

On the other hand, the description of the age structure of the population in the long run is also an interesting problem in population dynamics. Many models have been proposed and analyzed concerning single-species population growth with various stages of life history. Bibliographies can be found in [1, 2, 4, 17, 18, 28, 39–41].

It is the main purpose of this paper to propose and analyze a model of single-species population growth dispersing in a multi-patch environment, where individual

members of the population have a life history that takes them through two stages, immature and mature. Under the assumption that the dispersion of population between patches is symmetric, the subsystem for the mature population in our model is a cooperative and irreducible system of retarded functional differential equations with a discrete time delay representing the time from birth to maturity. By using the monotone dynamical systems theory of Hirsch [24] and Smith [36], we will show the persistence of the subsystem for the mature population and the existence as well as the global asymptotic stability of a positive equilibrium state. The subsystem for the immature population is a system of ordinary differential equations with a perturbation term representing the net flow of the birth from the mature population into immature population and the removal rate from immature population to mature population. We will show that this subsystem has a positive equilibrium state which is globally asymptotically stable.

We will also investigate the global convergence problem in the case of nonsymmetric dispersal of population between different patches by using a convergence theorem via limiting equations for general nonautonomous "regular" and "precompact" functional differential equations, representing an extension of a result due to Artstein [3] for nonautonomous ordinary differential equations to retarded equations.

We should mention that the global stability of the positive equilibrium state has been proved by Aiello and Freedman [1] for a model of a single-species population with stage structures where the population is assumed to be distributed over a homogeneous environment. For other related results, we refer to [1, 2] and references therein. Our results in this paper show that, as far as our model is concerned, the heterogeneity of the environment may change the size of the positive equilibrium state but cannot change its global asymptotic stability.

This paper is organized as follows. In Sec. 2, we develop our model and present some standing assumptions. In Sec. 3, we consider the global dynamics of both mature populations and immature populations in the case of symmetric dispersion of the population between patches. Section 4 contains a global convergence result in the case of nonsymmetric dispersion of the population between two patches. In Sec. 5, we briefly indicate how the approach employed in Sects. 3 and 4 can be effectively combined to establish the global asymptotic stability of a positive equilibrium state in a general multipatch environment with possible nonsymmetric dispersion.

2. Model equations. We suppose that the system is composed of n patches connected by dispersion and occupied by a single species. Let $I_i(t)$ and $M_i(t)$ denote the concentration of immature and mature populations in the ith patch, $i = 1, 2, \ldots, n$. To derive our model equations, we make the following assumptions.

(H1): The birth rate into the immature population in the ith patch is proportional to the existing mature population with proportionality constant $\alpha_i > 0$, $i = 1, \ldots, n$.

(H2): The death rate of the immature population in the ith patch is proportional to the existing immature population with proportionality constant $\gamma_i > 0$, $i = 1, \ldots, n$.

(H3): The death rate of the mature population in the ith patch is of a logistic nature, i.e., proportional to the square of the population with proportionality constant $\beta_i > 0$, $i = 1, \dots, n$.

(H4): The length of time from birth to maturity is a constant $\tau > 0$, which is uniform for each individual in all patches.

(H5): Those immature individuals born at time $t - \tau$ and surviving to time t exit from the immature population and enter into the mature population.

(H6): The net exchange of mature and immature populations from the jth patch to the ith patch is proportional to the difference of the concentrations $M_j(t) - M_i(t)$ and $I_j(t) - I_i(t)$, respectively, with proportionality constants $D_{ji} \geq 0$ and $\delta_{ji} \geq 0$, $i \neq j$, $i, j = 1, \dots, n$.

Under the above assumptions, we propose a model to describe the growth of a single-species population dispersing in an n patch environment where individual members of the population have a two-stage structure as follows

$$\frac{d}{dt}I_i(t) = -\gamma_i I_i(t) + \sum_{j \neq i} \delta_{ji}[I_j(t) - I_i(t)] + \alpha_i M_i(t) - x_i(t, t - \tau),$$

$$\frac{d}{dt}M_i(t) = -\beta_i M_i^2(t) + \sum_{j \neq i} D_{ji}[M_j(t) - M_i(t)] + x_i(t, t - \tau), \tag{2.1}$$

$$t \geq 0, \quad i = 1, \dots, n,$$

where for any s, $t - \tau \leq s \leq t$, $x_i(s, t - \tau)$ denotes the growth rate at the instant s of the immature population in the ith patch born at the instant $t - \tau$.

Obviously,

$$x_i(t - \tau, t - \tau) = \alpha_i M_i(t - \tau). \tag{2.2}$$

To derive an explicit formula for $x_i(s, t - \tau)$ in terms of $M_j(t)$, $j = 1, \dots, n$, we denote by $y_i(s, t - \tau)$, $t - \tau \leq s \leq t$, the total immature population in the ith patch born at the instant $t - \tau$. Then $\frac{\partial}{\partial s}y_i(s, t - \tau) = x_i(s, t - \tau)$ and we have the following relation

$$x_i(s, t - \tau) = -\gamma_i y_i(s, t - \tau) + \sum_{j \neq i} \delta_{ji}[y_j(s, t - \tau) - y_i(s, t - \tau)]$$

from which it follows that

$$\frac{\partial}{\partial s}y_i(s, t - \tau) = -\gamma_i y_i(s, t - \tau) + \sum_{j \neq i} \delta_{ji}[y_j(s, t - \tau) - y_i(s, t - \tau)], \tag{2.3}$$

$$t - \tau \leq s \leq t.$$

Let $A = (a_{ij})$ with

$$a_{ij} = \delta_{ji} \quad \text{for } i, j = 1, \dots, n, \ i \neq j,$$

and

$$a_{ii} = -\gamma_i - \sum_{j \neq i} \delta_{ji}, \qquad i = 1, \dots, n.$$

Then $a_{ij} \geq 0$ for $i \neq j$, and $\sum_{j=1}^{n} a_{ij} = -\gamma_i < 0$ for $i = 1, \ldots, n$. Therefore A^{-1} exists and for any $t \geq 0$, e^{At} is a matrix whose entries are nonnegative. Evidently, (2.3) can be rewritten as

$$\frac{\partial}{\partial s} \begin{pmatrix} y_1(s, t - \tau) \\ \vdots \\ y_n(s, t - \tau) \end{pmatrix} = A \begin{pmatrix} y_1(s, t - \tau) \\ \vdots \\ y_n(s, t - \tau) \end{pmatrix}$$

from which it follows that

$$\begin{pmatrix} y_1(s, t - \tau) \\ \vdots \\ y_n(s, t - \tau) \end{pmatrix} = e^{A(s-t+\tau)} \begin{pmatrix} y_1(t - \tau, t - \tau) \\ \vdots \\ y_n(t - \tau, t - \tau) \end{pmatrix}$$

and thus

$$\frac{\partial}{\partial s} \begin{pmatrix} y_1(s, t - \tau) \\ \vdots \\ y_n(s, t - \tau) \end{pmatrix} = A e^{A(s-t+\tau)} \begin{pmatrix} y_1(t - \tau, t - \tau) \\ \vdots \\ y_n(t - \tau, t - \tau) \end{pmatrix}. \tag{2.4}$$

Substituting (2.2) into (2.4), we get

$$\begin{pmatrix} \alpha_1 M_1(t - \tau) \\ \vdots \\ \alpha_n M_n(t - \tau) \end{pmatrix} = A \begin{pmatrix} y_1(t - \tau, t - \tau) \\ \vdots \\ y_n(t - \tau, t - \tau) \end{pmatrix}.$$

Consequently,

$$\begin{pmatrix} y_1(t - \tau, t - \tau) \\ \vdots \\ y_n(t - \tau, t - \tau) \end{pmatrix} = A^{-1} \begin{pmatrix} \alpha_1 M_1(t - \tau) \\ \vdots \\ \alpha_n M_n(t - \tau) \end{pmatrix}$$

and

$$\frac{\partial}{\partial s} \begin{pmatrix} y_1(s, t - \tau) \\ \vdots \\ y_n(s, t - \tau) \end{pmatrix} = A e^{A(s-t+\tau)} A^{-1} \begin{pmatrix} \alpha_1 M_1(t - \tau) \\ \vdots \\ \alpha_n M_n(t - \tau) \end{pmatrix} = e^{A(s-t+\tau)} \begin{pmatrix} \alpha_1 M_1(t - \tau) \\ \vdots \\ \alpha_n M_n(t - \tau) \end{pmatrix}.$$

Therefore

$$\begin{pmatrix} x_1(t, t - \tau) \\ \vdots \\ x_n(t, t - \tau) \end{pmatrix} = \frac{\partial}{\partial s} \begin{pmatrix} y_1(s, t - \tau) \\ \vdots \\ y_n(s, t - \tau) \end{pmatrix} \Bigg|_{s=t} = e^{A\tau} \begin{pmatrix} \alpha_1 M_1(t - \tau) \\ \vdots \\ \alpha_n M_n(t - \tau) \end{pmatrix}.$$

Let $e^{A\tau} = (b_{ij})$. Then $b_{ij} \geq 0$ for $i, j = 1, \ldots, n$ and

$$x_i(t, t - \tau) = \sum_{j=1}^{n} b_{ij} \alpha_j M_j(t - \tau)$$

from which our model equation (2.1) can be reduced to the following form

$$\begin{cases} \frac{d}{dt} I_i(t) = -\gamma_i I_i(t) + \sum_{j \neq i} \delta_{ji}[I_j(t) - I_i(t)] + \alpha_i M_i(t) - \sum_{j=1}^{n} b_{ij} \alpha_j M_j(t - \tau), \\ \frac{d}{dt} M_i(t) = -\beta_i M_i^2(t) + \sum_{j \neq i} D_{ji}[M_j(t) - M_i(t)] + \sum_{j=1}^{n} b_{ij} \alpha_j M_j(t - \tau), \end{cases} \tag{2.5}$$

for $t \geq 0$ and $i = 1, \ldots, n$.

To specify a solution of the model equation (2.5), we assume that the distribution of the mature population over the initial period $-\tau \leq t \leq 0$ is given as follows

$$M_i(\theta) = \varphi_i(\theta), \qquad -\tau \leq \theta \leq 0, \ i = 1, 2, \ldots, n, \qquad (2.6)$$

and the immature population at $t = 0$ is given as follows

$$I_i(0) = I_{i0}, \qquad i = 1, 2, \ldots, n, \qquad (2.7)$$

where $\varphi_i(\theta)$ is a nonnegative continuous function on $[-\tau, 0]$ and I_{i0} is a given nonnegative constant, $i = 1, \ldots, n$.

3. Persistence and global convergence in the case of symmetric dispersal. In this section, we consider the global dynamics of our model equation (2.5) under the following assumption concerning the dispersion between different patches.

(H7): The dispersion matrices $D = (D_{ij})$ and $\Delta = (\delta_{ij})$, where $\delta_{ii} = D_{ii} = 0$, $i = 1, \ldots, n$ are irreducible.

We begin by considering the subsystem for the mature populations

$$\frac{d}{dt} M_i(t) = -\beta_i M_i^2(t) + \sum_{j \neq i} D_{ji}[M_j(t) - M_i(t)] + \sum_{j=1}^{n} b_{ij} \alpha_j M_j(t - \tau) \qquad (3.1)$$

where $t \geq 0$, $i = 1, \ldots, n$. Let $C_n = C([-\tau, 0]; R^n)$ and $C_n^+ = \{\varphi \in C_n; \varphi = (\varphi_1, \ldots, \varphi_n), \varphi_i(\theta) \geq 0$ for $i = 1, \ldots, n$ and $\theta \in [-\tau, 0]\}$. Define $F = (F_1, \ldots, F_n): C_n \to R^n$ by

$$F_i(\varphi) = -\beta_i \varphi_i^2(0) + \sum_{j \neq i} D_{ji}[\varphi_j(0) - \varphi_i(0)] + \sum_{j=1}^{n} b_{ij} \alpha_j \varphi_j(-\tau), \qquad i = 1, \ldots, n,$$

where $\varphi \in C_n$. It is easy to verify the following quasimonotonicity condition: for any $\varphi \in C_n^+$, if $\varphi_i(0) = 0$, then $F_i(\varphi) \geq 0$. Therefore, by Corollary 2.1 of Smith [36], C_n^+ is positively invariant, i.e., for any $\varphi \in C_n^+$, $M_i(t, \varphi) \geq 0$ for $t \geq 0$ and $i = 1, \ldots, n$, where $M(t, \varphi) = (M_1(t, \varphi), \ldots, M_n(t, \varphi))$ is the unique solution of (3.1) satisfying $M_i(\theta, \varphi) = \varphi_i(\theta)$ for $\theta \in [-\tau, 0]$ and $i = 1, \ldots, n$.

The following result indicates that all solutions of system (3.1) are bounded.

LEMMA 3.1. *For any $\varphi \in C_n^+$, we have*

$$0 \leq M_i(t, \varphi) \leq L(\varphi), \qquad t \geq 0, \ i = 1, \ldots, n,$$

where

$$L(\varphi) = \max\left\{ \max_{-\tau \leq \theta \leq 0} \max_{i=1,\ldots,n} \varphi_i(\theta), \ \max_{i=1,\ldots,n} \frac{\sum_{j=1}^{n} b_{ij}\alpha_j}{\beta_i} + 1 \right\}.$$

Proof. Let

$$V(t) = \max\left\{ \max_{-\tau \leq \theta \leq t} \max_{i=1,\ldots,n} M_i(\theta, \varphi), \ \max_{i=1,\ldots,n} \frac{\sum_{j=1}^{n} b_{ij}\alpha_j}{\beta_i} + 1 \right\}.$$

For any given $t \geq 0$, if $\max_{i=1,\ldots,n} M_i(t, \varphi) < V(t)$, then clearly $D^+ V(t) = 0$, where

$$D^+ V(t) = \limsup_{h \to 0^+} \frac{V(t+h) - V(t)}{h}.$$

If $\max_{1,\ldots,n} M_i(t,\varphi) = V(t)$, then for any $j \notin J := \{k : M_k(t,\varphi) = V(t)\}$, $M_j(t+h,\varphi) < M_k(t+h,\varphi)$ for any $k \in J$ and sufficiently small $h \geq 0$. Select a sequence $h_m \to 0^+$ such that

$$D^+V(t) = \lim_{m \to \infty} \frac{V(t+h_m) - V(t)}{h_m}.$$

Then two cases may occur:

CASE 1. There are infinitely many h_m's such that $V(t+h_m) \leq V(t)$.

In this case, it is clear that $D^+V(t) \leq 0$.

CASE 2. There are only finitely many h_m's such that $V(t+h_m) \leq V(t)$.

In this case, there exist a $k \in J$ and a sequence $\{h_m^*\}$ with $0 < h_m^* \leq h_m$ such that $V(t+h_m) = M_k(t+h_m^*,\varphi)$. Therefore

$$D^+V(t) = \lim_{m \to \infty} \frac{M_k(t+h_m^*,\varphi) - M_k(t,\varphi)}{h_m}. \tag{3.2}$$

Note that

$$\lim_{m \to \infty} \frac{M_k(t+h_m^*,\varphi) - M_k(t,\varphi)}{h_m^*}$$

$$= \frac{d}{dt} M_k(t,\varphi)$$

$$= -\beta_k M_k^2(t,\varphi) + \sum_{j \neq k} D_{jk}[M_j(t,\varphi) - M_k(t,\varphi)] + \sum_{j=1}^{n} b_{kj}\alpha_j M_j(t-\tau,\varphi) .$$

$$\leq -\beta_k M_k^2(t,\varphi) + \sum_{j=1}^{n} b_{kj}\alpha_j M_j(t-\tau,\varphi)$$

$$\leq \left[\frac{\sum_{j=1}^{n} b_{kj}\alpha_j}{\beta_k} - M_k(t,\varphi) \right] \beta_k M_k(t,\varphi) < 0.$$

Therefore, $M_k(t+h_m^*,\varphi) < M_k(t,\varphi)$ for sufficiently large m, from which result together with (3.2) it follows that $D^+V(t) \leq 0$.

Therefore for any $t \geq 0$, $D^+V(t) \leq 0$ holds. By the well-known result of differential inequalities (see, e.g., [28]), we obtain $V(t) \leq V(0)$ for $t \geq 0$, from which our conclusion follows. This completes the proof.

The following result shows a dissipative property of system (3.1).

LEMMA 3.2. There exists a constant $B > 0$ such that for any $\varphi \in C_n^+$, we have

$$\limsup_{t \to \infty}[M_1(t,\varphi) + \cdots + M_n(t,\varphi)] < B.$$

Proof. Let $\rho > 1$ be a given constant and

$$M = \frac{n^2(\rho \max_{i=1,\ldots,n} \max_{j=1,\ldots,n} b_{ij}\alpha_j + \max_{i=1,\ldots,n} \max_{j \neq i} D_{ji})}{\min_{i=1,\ldots,n} \beta_i}.$$

Define $M_i(t) = M_i(t, \varphi)$ and $W(t) = \sum_{i=1}^{n} M_i(t)$. Then

$$\dot{W}(t) = \sum_{i=1}^{n} \left[-\beta_i M_i^2(t) + \sum_{j \neq i} D_{ji}(M_j(t) - M_i(t)) + \sum_{j=1}^{n} b_{ij} \alpha_j M_j(t - \tau) \right]$$

$$\leq -(\min_{i=1,\dots,n} \beta_i) \sum_{i=1}^{n} M_i^2(t) + n(\max_{i=1,\dots,n} \max_{j \neq i} D_{ji}) W(t)$$

$$+ n \max_{i=1,\dots,n} \max_{j=1,\dots,n} b_{ij} \alpha_j W(t - \tau)$$

$$\leq -\frac{\min_{i=1,\dots,n} \beta_i}{n} W^2(t) + n(\max_{i=1,\dots,n} \max_{j \neq i} D_{ji}) W(t)$$

$$+ n \max_{i=1,\dots,n} \max_{j=1,\dots,n} b_{ij} \alpha_j W(t - \tau).$$

Therefore, if $W(t - \tau) \leq \rho W(t)$ and $W(t) > M$, then

$$\dot{W}(t) \leq \left[\frac{n^2 (\max_{i=1,\dots,n} \max_{j \neq i} D_{ji} + \rho \max_{i=1,\dots,n} \max_{j=1,\dots,n} b_{ij} \alpha_j)}{\min_{i=1,\dots,n} \beta_i} - W(t) \right]$$

$$\times W(t) \frac{\min_{i=1,\dots,n} \beta_i}{n} < 0.$$

Therefore by the classical Liapunov-Razumikhin theorem for uniformly ultimate boundedness (see, e.g., [21]), there exists a constant $B > 0$ uniformly for all $\varphi \in C_n^+$ such that $\lim_{t \to \infty} \sup \sum_{i=1}^{n} M_i(t, \varphi) < \beta$. This completes the proof.

By the general dissipative dynamical systems theory (see, e.g., [22]) system (3.1) has a globally compact attractor. We want to show that this attractor contains at least one positive equilibrium point. To provide a tool for the study of the existence and stability problem of equilibria, we briefly describe a result due to Smith [36].

Suppose $f : C_n \to R^n$ is continuously differentiable such that for any $\varphi \in C_n$ there exists one and only one solution of the following initial value problem

$$\begin{cases} \dfrac{d}{dt} x(t) = f(x_t), & t \geq 0, \\ x_0 = \varphi. \end{cases} \tag{3.3}$$

Let $x(t, \varphi)$ be the unique solution. We obtain a semiflow $\{T(t)\}_{t \geq 0}$ defined on C_n as follows

$$T(t)\phi = x_t(\phi) \quad \text{for } t \geq 0 \text{ and } \varphi \in C_n.$$

Denote by $df(\psi)$ the Frechlet derivative of f at ψ. Then by the Riesz representation theorem we have the following standard representation

$$df(\psi)\phi = \sum_{j=1}^{n} \int_{-\tau}^{0} \phi_j(\theta) \, d\eta_{ij}(\psi, \theta),$$

where for each $\psi \in C_n, \eta_{ij}(\psi, \cdot) : R \to R$ satisfies $\eta_{ij}(\psi, \theta) = \eta_{ij}(\psi, 0)$ for $\theta \geq 0$, $\eta_{ij}(\psi, \theta) = 0$ for $\theta \leq -\tau$, $\eta_{ij}(\psi, \cdot)$ is of bounded variation on $[-\tau, 0]$ and

is continuous from the left on $[-\tau, 0]$, $i, j = 1, \ldots, n$. We say f is cooperative and irreducible in C_n^+, if for any $\psi \in C_n^+$ the following conditions are satisfied.

(i) For any $\phi \in C_n^+$ with $\varphi_i(0) = 0$, it follows that $\sum_{j=1}^{n} \int_{-\tau}^{0} \phi_j(\theta) d\eta_{ij}(\psi, \theta) \geq 0$.

(ii) The matrix $(df(\psi)\hat{e}_1, \ldots, df(\psi)\hat{e}_n)$ is irreducible, where $\{e_1, \ldots, e_n\}$ denotes the standard basis in R^n and $\hat{}$ denotes the inclusion $R^n \to C_n$ by $x \to \hat{x}$, $\hat{x}_i(\theta) = x_i$ for $\theta \in [-\tau, 0]$ and $i = 1, \ldots, n$.

(iii) For every j there exists i such that for all $\psi \in C_n^+$ and all small positive ε, $\eta_{ij}(\psi, -\tau + \varepsilon) > 0$.

In Smith [36] the following result is proved.

LEMMA 3.3. Let f be cooperative and irreducible in C_n^+. Then the semiflow $\{T(t)\}_{t \geq 0}$ defined on C_n^+ is monotone and eventually strongly monotone. That is,

(i) if $\psi - \phi \in C_n^+$, then $x_t(\psi) - x_t(\phi) \in C_n^+$ for $t \geq 0$;

(ii) if $\psi - \phi \in C_n^+ \setminus \{0\}$, then $x_t(\psi) - x_t(\phi) \in \text{Int}\, C_n^+$ for $t \geq (n + 1)\tau$.

As an application of the above result, we obtain the following result concerning the persistence of system (3.1).

THEOREM 3.1. For any $\phi \in C_n^+ \setminus \{0\}$, we have $\liminf_{t \to \infty} M_i(t, \varphi) > 0$ for $i = 1, \ldots, n$.

Proof. It is clear that $F : C_n \to R^n$ is continuously differentiable. For any $\psi \in C_n^+$ and $\varphi \in C_n$, we have

$$dF_i(\psi)\phi = -2\beta_i \psi_i(0)\phi_i(0) + \sum_{j \neq i} D_{ji}[\phi_j(0) - \phi_i(0)] + \sum_{j=1}^{n} b_{ij}\alpha_j\phi_j(-\tau),$$

where $i = 1, \ldots, n$ and $dF(\psi) = (dF_1(\psi), \ldots, dF_n(\psi))$. Therefore we have the following observations.

(i) $dF_i(\psi)\phi \geq 0$ if $\phi \in C_n^+$ and $\phi_i(0) = 0$.

(ii) The matrix

$(dF(\psi)\hat{e}_1, \ldots, dF(\psi)\hat{e}_n) =$
$$\begin{bmatrix} -2\beta_1\psi_1(0) - \sum_{j \neq 1} D_{j1} + b_{11}\alpha_1 & D_{21} + b_{12}\alpha_2 & \cdots & D_{n1} + b_{1n}\alpha_n \\ D_{12} + b_{21}\alpha_1 & -2\beta_2\psi_2(0) - \sum_{j \neq 2} D_{j2} + b_{22}\alpha_2 & & D_{n2} + b_{2n}\alpha_n \\ \vdots & \vdots & & \vdots \\ D_{1n} + b_{n1}\alpha_1 & D_{2n} + b_{n2}\alpha_2 & & -2\beta_n\psi_n(0) - \sum_{j \neq n} D_{jn} + b_{nn}\alpha_n \end{bmatrix}$$

is irreducible, since by assumption (H7), the diffusion matrix D is irreducible and the matrix $e^{A\tau} = (b_{ij})$ is positive.

Therefore, F is cooperative and irreducible in C_n^+. By Lemma 3.3, we know that if $\phi \in C_n^+ \setminus \{0\}$, then $M_i(t, \varphi) > 0$ for $t \geq n\tau$ and $i = 1, \ldots, n$. To prove the theorem, it suffices to verify that if $\varepsilon > 0$ is sufficiently small, then the set $C_n^+(\varepsilon) = \{\varphi \in C_n^+ ; \varphi_i(\theta) \geq \varepsilon$ for $\theta \in [-\tau, 0]$ and $i = 1, \ldots, n\}$ is positively invariant, i.e., if $\varphi \in C_n^+(\varepsilon)$ then $M_i(t, \varphi) \geq \varepsilon$ for $t \geq 0$ and $i = 1, \ldots, n$. This is

true for any ε with $0 < \varepsilon < min_{i=1,\dots,n}(\sum_{j=1}^{n} b_{ij}\alpha_j)/\beta_i$, since for any $\varphi \in C_n^+(\varepsilon)$ if $\varphi_i(0) = \varepsilon$ for some i, then

$$F_i(\phi) = -\beta_i\varepsilon^2 + \sum_{j\neq i} D_{ji}[\varphi_j(0) - \phi_i(0)] + \sum_{j=1}^{n} b_{ij}\alpha_j\varphi_j(-\tau)$$

$$\geq -\beta_i\varepsilon^2 + \sum_{j\neq i} D_{ji}[\varphi_j(0) - \varepsilon] + \sum_{j=1}^{n} b_{ij}\alpha_j\varepsilon$$

$$= \left(-\beta_i\varepsilon + \sum_{j=1}^{n} b_{ij}\alpha_j\right)\varepsilon \geq 0$$

(see, e.g. [30]). The proof is then completed.

We will show that the persistence implies the existence, uniqueness, and global asymptotic stability of a positive equilibrium state. To show this, we need the following result due to Hirsch [24].

LEMMA 3.4. Suppose $\widetilde{F} = (\widetilde{F}_1, \dots, \widetilde{F}_n)$ is a C^1 vector field in R^n satisfying the following conditions.

(i) The off-diagonal elements of the Jacobian $D\widetilde{F}(x)$ of $\widetilde{F}(x)$ are nonnegative for any $x \in R_+^n := \{x \in R^n : x = (x_1, \dots, x_n), x_i \geq 0, i = 1, \dots, n\}$.

(ii) $D\widetilde{F}(x)$ is irreducible for any $x \in R_+^n$.

(iii) $D\widetilde{F}(y) - D\widetilde{F}(x) \in R_+^{n\times n}$ for any $x, y \in R_+^n$ with $x - y \in R_+^n$.

(iv) All solutions in R_+^n of the system $\dot{x} = \widetilde{F}(x)$ are bounded.

Then either trajectories in R_+^n tend to the origin, or else there is a unique equilibrium $p \in \text{Int } R_+^n$ and all trajectories in $R_+^n \setminus \{0\}$ tend to p.

THEOREM 3.2. System (3.1) has one and only one positive equilibrium. This positive equilibrium is globally asymptotically stable over $C_n^+ \setminus \{0\}$.

Proof. According to the proof of Theorem 3.1, the set $C_n^+(\varepsilon) = \{\varphi \in C_n^+ : \varphi_i(\theta) \geq \varepsilon$ for $\theta \in [-\tau, 0], i = 1, \dots, n\}$ is positively invariant for any ε with $0 < \varepsilon < \min_{i=1,\dots,n}\{(\sum_{j=1}^{n} b_{ij}\alpha_j)/\beta_i\}$. Lemma 3.2 shows that system (3.1) is point dissipative. Therefore, by Theorem 4.1.2 of [23], there is a global attractor G_ε in $C_n^+(\varepsilon)$. Since for a strongly monotone dynamical system, the global attractor contains at least one equilibrium point (see, e.g., Theorem 3.1 of [24]), G_ε contains at least one equilibrium. Therefore, system (3.1) has at least one positive equilibrium state.

We now consider the ordinary differential equations

$$\dot{x}_i = \sum_{j=1}^{n} b_{ij}\alpha_j x_j - \beta_i x_i^2 + \sum_{j\neq i} D_{ji}(x_j - x_i), \qquad i = 1, \dots, n. \qquad (3.4)$$

Let $\widetilde{F} = (\widetilde{F}_1, \dots, \widetilde{F}_n) : R^n \to R^n$ be defined by

$$\widetilde{F}_i = \sum_{j=1}^{n} b_{ij}\alpha_j x_j - \beta_i x_i^2 + \sum_{j\neq i} D_{ji}(x_j - x_i), \qquad i, \dots, n.$$

Obviously, $\frac{\partial \widetilde{F}_i}{\partial x_j}(x_1, \dots, x_n) = b_{ij}\alpha_j + D_{ji} \geq 0$ for $i \neq j$, $D\widetilde{F}(x)$ is irreducible for $x \in R_+^n$, since the dispersal matrix (D_{ij}) is irreducible. Moreover, it is easy to verify that $D\widetilde{F}(y) - D\widetilde{F}(x) \in R_+^{n \times n}$ if x, $y \in R_+^n$ and $x - y \in R_+^n$. Employing the same argument as that for Lemma 3.1, we can prove that all nonnegative solutions of (3.4) are bounded. Therefore by Lemma 3.4, either there is no positive equilibrium and the origin is globally asymptotically stable, or there is a unique positive equilibrium which is globally asymptotically stable over $R_+^n \setminus \{0\}$.

On the other hand, we have shown that system (3.1) has at least one positive equilibrium. Clearly, any equilibrium of system (3.1) is also an equilibrium for system (3.4) and conversely. Therefore, (3.4), and hence (3.1), has one and only one positive equilibrium.

This unique positive equilibrium, denoted by P, of system (3.1) must be in $C_n^+(\varepsilon)$ for any ε with $0 < \varepsilon < \min_{i=1,\dots,n}(\sum_{j=1}^n b_{ij}\alpha_j)/\beta_i$. By Theorem 3.3 of [25], $\lim_{t\to\infty} M_t(\phi) = P$ for any $\phi \in C_n^+(\varepsilon)$. This implies that $\lim_{t\to\infty} M_t(\phi) = P$ for any $\phi \in C_n^+ \setminus \{0\}$ since, by Theorem 3.1, for any $\phi \in C_n^+ \setminus \{0\}$ there exists $\varepsilon > 0$ such that $M_t(\phi) \in C_n^+(\varepsilon)$ for sufficiently large t. The proof is then completed.

We now consider the subsystem for the immature population

$$\frac{d}{dt}I_i(t) = -\gamma_i I_i(t) + \sum_{j \neq i} \delta_{ji}[I_j(t) - I_i(t)] + \alpha_i M_i(t) - \sum_{j=1}^n b_{ij}\alpha_j M_j(t-\tau),$$
$$i = 1, \dots, n. \quad (3.5)$$

We have the following global convergence theorem.

THEOREM 3.3. Suppose that the initial mature population $(\varphi_1, \dots, \varphi_n) \in C_n^+$ and

$$\begin{pmatrix} I_1(0) \\ \vdots \\ I_n(0) \end{pmatrix} \geq \int_{-\tau}^0 e^{-As} \begin{pmatrix} \alpha_1 \varphi_1(s) \\ \vdots \\ \alpha_n \varphi_n(s) \end{pmatrix} ds.$$

Then $I_i(t) \geq 0$ for $t \geq 0$ and $i = 1, \dots, n$. If, in addition, $(\varphi_1, \dots, \varphi_n) \in C_n^+ \setminus \{0\}$, then

$$\lim_{t\to\infty} \begin{pmatrix} I_1(t) \\ \vdots \\ I_n(t) \end{pmatrix} = A^{-1}(e^{A\tau} - I) \begin{pmatrix} \alpha_1 M_1^* \\ \vdots \\ \alpha_n M_n^* \end{pmatrix},$$

where $(M_1^*, \dots, M_n^*)$ is the unique positive equilibrium of system (3.1).

Proof. Equation (3.5) can be rewritten in the following vector form

$$\frac{d}{dt} \begin{pmatrix} I_1(t) \\ \vdots \\ I_n(t) \end{pmatrix} = A \begin{pmatrix} I_1(t) \\ \vdots \\ I_n(t) \end{pmatrix} + \begin{pmatrix} \alpha_1 M_1(t) \\ \vdots \\ \alpha_n M_n(t) \end{pmatrix} - e^{A\tau} \begin{pmatrix} \alpha_1 M_1(t-\tau) \\ \vdots \\ \alpha_n M_n(t-\tau) \end{pmatrix}.$$

Therefore,

$$\frac{d}{dt}\left[e^{-At}\begin{pmatrix}I_1(t)\\\vdots\\I_n(t)\end{pmatrix}\right] = e^{-At}\left[\frac{d}{dt}\begin{pmatrix}I_1(t)\\\vdots\\I_n(t)\end{pmatrix} - A\begin{pmatrix}I_1(t)\\\vdots\\I_n(t)\end{pmatrix}\right]$$

$$= e^{-At}\left[\begin{pmatrix}\alpha_1 M_1(t)\\\vdots\\\alpha_n M_n(t)\end{pmatrix} - e^{A\tau}\begin{pmatrix}\alpha_1 M_1(t-\tau)\\\vdots\\\alpha_n M_n(t-\tau)\end{pmatrix}\right]$$

$$= \frac{d}{dt}\int_{t-\tau}^t e^{-As}\begin{pmatrix}\alpha_1 M_1(s)\\\vdots\\\alpha_n M_n(s)\end{pmatrix} ds,$$

from which it follows that

$$e^{-At}\begin{pmatrix}I_1(t)\\\vdots\\I_n(t)\end{pmatrix} - \int_{t-\tau}^t e^{-As}\begin{pmatrix}\alpha_1 M_1(s)\\\vdots\\\alpha_n M_n(s)\end{pmatrix} ds = \begin{pmatrix}I_1(0)\\\vdots\\I_n(0)\end{pmatrix} - \int_{-\tau}^0 e^{-As}\begin{pmatrix}\alpha_1 M_1(s)\\\vdots\\\alpha_n M_n(s)\end{pmatrix} ds.$$

That is,

$$\begin{pmatrix}I_1(t)\\\vdots\\I_n(t)\end{pmatrix} = e^{At}\left[\begin{pmatrix}I_1(0)\\\vdots\\I_n(0)\end{pmatrix} - \int_{-\tau}^0 e^{-As}\begin{pmatrix}\alpha_1\varphi_1(s)\\\vdots\\\alpha_n\varphi_n(s)\end{pmatrix} ds\right] + \int_0^\tau e^{A\theta}\begin{pmatrix}\alpha_1 M_1(t-\theta)\\\vdots\\\alpha_n M_n(t-\theta)\end{pmatrix} d\theta.$$

Therefore our conclusion follows from the fact that e^{At} is a positive matrix for $t > 0$, $e^{At} \to 0$ as $t \to \infty$,

$$\begin{pmatrix}\alpha_1 M_1(t)\\\vdots\\\alpha_n M_n(t)\end{pmatrix} \geq \begin{pmatrix}0\\\vdots\\0\end{pmatrix} \quad \text{for } t \geq -\tau,$$

$$\begin{pmatrix}\alpha_1 M_1(t)\\\vdots\\\alpha_n M_n(t)\end{pmatrix} \to \begin{pmatrix}\alpha_1 M_1^*\\\vdots\\\alpha_n M_n^*\end{pmatrix} \quad \text{as } t \to \infty,$$

and the following relation

$$\int_0^\tau e^{A\theta}\begin{pmatrix}\alpha_1 M_1^*\\\vdots\\\alpha_n M_n^*\end{pmatrix} d\theta = \int_0^\tau A^{-1}\frac{d}{d\theta}e^{A\theta}\begin{pmatrix}\alpha_1 M_1^*\\\vdots\\\alpha_n M^*\end{pmatrix} = A^{-1}(e^{A\tau}-I)\begin{pmatrix}\alpha_1 M_1^*\\\vdots\\\alpha_n M_n^*\end{pmatrix}.$$

REMARK 3.1. To conclude this section, we remark that in the case of symmetric dispersal, i.e., $D_{ij} = 0$ iff $\delta_{ij} = 0$ and $D_{ij} = 0$ iff $D_{ji} = 0$ for $i \neq j$, the assumption (H7) can be dropped, since if D or Δ is reducible, then the subsystem for the mature population in Eq. (2.5) decouples into two or more smaller irreducible subsystems, and consequently our results in this section can be applied to these irreducible subsystems.

4. Convergence in the case of nonsymmetric dispersion: a two-patch environment.
We have considered a single-species population with two life stages which disperses
in a multi-patch environment. In the case of symmetric dispersion between different
patches, we showed that the subsystem for the mature population can be decoupled
into smaller subsystems which are described by cooperative and irreducible retarded
functional differential equations, with the time delay representing the time from
birth to maturity. By using the monotone dynamical systems theory due to Hirsch
and Smith, we proved that there exists one and only one positive equilibrium point
which is globally asymptotically stable.

However, the nonsymmetric case is much more complicated even for the model
describing a single-species population dispersing in a two-patch environment with
$\delta_{21} = D_{21} = 0$.

In this case,

$$A = \begin{pmatrix} -\gamma_1 & 0 \\ \delta_{12} & -\gamma_2 - \delta_{12} \end{pmatrix}$$

and

$$e^{At} = \begin{pmatrix} e^{-\gamma_1 t} & 0 \\ e^{-(\gamma_2+\delta_{12})t} & \int_0^t e^{-(\gamma_2+\delta_{12})(t-s)}\delta_{12}e^{-\gamma_1 s}\,ds \end{pmatrix} .$$

Therefore,

$$(b_{ij}) = \begin{pmatrix} e^{-\gamma_1 \tau} & 0 \\ e^{-(\gamma_2+\delta_{12})\tau} & \int_0^\tau e^{-(\gamma_2+\delta_{12})(\tau-s)}\delta_{12}e^{-\gamma_1 s}\,ds \end{pmatrix} .$$

In particular, $b_{12} = 0$. Hence the model equation (2.5) becomes

$$
\begin{aligned}
\frac{dI_1(t)}{dt} &= -\gamma_1 I_1(t) + \alpha_1 M_1(t) - e^{-\gamma_1 \tau}\alpha_1 M_1(t-\tau), \\
\frac{dI_2(t)}{dt} &= -\gamma_2 I_2(t) + \delta_{12}[I_1(t)-I_2(t)] + \alpha_2 M_2(t) - b_{21}\alpha_1 M_1(t-\tau) - b_{22}\alpha_2 M_2(t-\tau), \\
\frac{dM_1(t)}{dt} &= -\beta_1 M_1^2(t) + e^{-\gamma_1 \tau}\alpha_1 M_1(t-\tau), \\
\frac{dM_2(t)}{dt} &= -\beta_2 M_2^2(t) + D_{12}[M_1(t)-M_2(t)] + b_{21}\alpha_1 M_1(t-\tau) + b_{22}\alpha_2 M_2(t-\tau).
\end{aligned}
$$

$$(4.1)$$

Because of the nonsymmetric dispersion among different patches, the vector field
for the subsystem of the mature population is no longer cooperative and irreducible
in the sense of Smith [36]. However, we can employ a similar argument to that of
Sec. 3 to prove that for any $\varphi_1 \in C([-\tau, 0], [0, \infty))$, if $\varphi_1 \not\equiv 0$, then the solution
$M_1(t)$ of the following initial value problem

$$
\begin{aligned}
\frac{d}{dt}M_1(t) &= \alpha_1 M_1(t-\tau)e^{-\gamma_1 \tau} - \beta_1 M_1^2(t) \\
M_1(\theta) &= \varphi_1(\theta), \qquad \theta \in [-\tau, 0]
\end{aligned}
$$

$$(4.2)$$

satisfies $\lim_{t\to\infty} M_1(t) = (\alpha_1 e^{-\gamma_1 \tau})/\beta_1$.

Applying this result to the fourth equation in system (4.1) we obtain an autonomous system

$$\frac{d}{dt}m_2(t) = -\beta_2 m_2^2(t) + D_{12}\frac{\alpha_1 e^{-\gamma_1\tau}}{\beta_1} - D_{12}m_2(t)$$

$$+ b_{21}\alpha_1\frac{\alpha_1 e^{-\gamma_1\tau}}{\beta_1} + b_{22}\alpha_2 m_2(t-\tau) \qquad (4.3)$$

as a limiting equation of

$$\frac{d}{dt}M_2(t) = -\beta_2 M_2^2(t) + D_{12}M_1(t) - D_{12}M_2(t)$$

$$+ b_{21}\alpha_1 M_1(t-\tau) + b_{22}\alpha_2 M_2(t-\tau). \qquad (4.4)$$

It is easy to show that there exists one and only one positive value M_2^* such that

$$-\beta_2 M_2^{*2} + D_{12}\frac{\alpha_1 e^{-\gamma_1\tau}}{\beta_1} - D_{12}M_2^* + b_{21}\alpha_1\frac{\alpha_1 e^{-\gamma_1\tau}}{\beta_1} + b_{22}\alpha_2 M_2^* = 0. \qquad (4.5)$$

Evidently, M_2^* is an equilibrium of (4.3). By using a similar argument to that in Sec. 3, we can prove that $m_2(t) \to M_2^*$ as $t \to \infty$ if $m_2(\theta) \geq 0$ for $\theta \in [-\tau, 0]$. To prove that $\lim_{t\to\infty} M_2(t) = M_2^*$ for any solution of (4.4) with $M_2 \in C_1^+$, we need the following global convergence theorem via limiting equations, as an extension of a result in [3] to retarded equations.

We consider a nonautonomous retarded equation

$$\dot{x}(t) = f(t, x_t) \qquad (4.6)$$

where $f : [0, \infty) \times C([-\tau, 0], R^n) \to R^n$ is continuous. Suppose that $U \subset C([-\tau, 0], R^n)$ is a given closed set such that for any $\varphi \in U$ and $t_0 \geq 0$, the solution of (4.6) with $x_{t_0} = \varphi$ exists uniquely for all $t \geq t_0$ and $x_t^f(t_0, \varphi) \in U$, where $x_t^f(t_0, \varphi)$ denotes the solution of (4.6) with $x_{t_0}^f(t_0, \varphi) = \varphi$. We say f is *positively precompact* with respect to U if, for any sequence $t_j \to \infty$ there exists a subsequence t_{j_k} and a continuous functional $g : [0, \infty) \times U \to R^n$ such that $f(t_{j_k} + t, \varphi) \to g(t, \varphi)$ as $k \to \infty$ uniformly for $(t, \varphi) \in [0, \infty) \times U$. Let

$$H(f) = \{g : [0, \infty) \times U \to R^n : g \text{ is continuous}$$

$$\text{and there exists a sequence } t_k \to \infty \text{ such that}$$

$$f(t_k + t, \varphi) \to g(t, \varphi) \text{ uniformly for}(t, \varphi) \in [0, \infty) \times U\}.$$

We say that f is *regular* if, for any $g \in H(f)$ and $(t_0, \varphi) \in [0, \infty) \times U$, the initial value problem $\dot{x}(t) = g(t, x_t)$, $x_{t_0} = \varphi$ has a unique solution, denoted by $x_t^g(t_0, \varphi)$, defined for all $t \geq t_0$ and $x_t^g(t_0, \varphi) \in U$ for all $t \geq t_0$.

THEOREM 4.1. Suppose that f is positively precompact and regular with respect to U, and that

(i) there exists a vector $K \in R^n$ such that the constant functional $\widehat{K} : [-\tau, 0] \to R^n$ defined by $\widehat{K}(\theta) = K$ for $\theta \in [-\tau, 0]$ belongs to U and $x_t^g(t_0, \varphi) \to \widehat{K}$ for $(t_0, \varphi) \in [0, \infty) \times U$ and for every $g \in H(f)$ as $t \to \infty$;

(ii) $\widehat{K}$ is eventually uniformly stable with respect to system (4.6) and U, namely, for any $\varepsilon > 0$ there exists $\delta(\varepsilon) > 0$ and $T(\varepsilon) > 0$ such that for any $(t_0, \varphi) \in [0, \infty) \times U$, if there exists $t^* \geq t_0 + T(\varepsilon)$ such that $\|x^f_{t^*}(t_0, \varphi) - \widehat{K}\| \leq \delta$ then $\|x^f_t(t_0, \varphi) - \widehat{K}\| \leq \varepsilon$ for $t \geq t^*$.

Then for any $(t_0, \varphi) \in [0, \infty) \times U$ such that $\{x^f_t(t_0, \varphi) : t \geq t_0\}$ has compact closure, it follows that $\lim_{t \to \infty} x^f_t(t_0, \varphi) = \widehat{K}$.

Proof. By way of contradiction, if the conclusion is not true, then there exist $(t_0, \varphi) \in [0, \infty) \times U$, $\varepsilon > 0$ and an increasing and unbounded sequence $t_k \to \infty$ as $k \to \infty$ such that $\|x^f_{t_k}(t_0, \varphi) - \widehat{K}\| \geq \varepsilon$ for $k \geq 1$. By assumption (ii), $\|x^f_t(t_0, \varphi) - \widehat{K}\| \geq \delta(\varepsilon)$ for all $t \geq t_0 + T(\varepsilon)$. Let $y^k(t) = x^f(t_k + t; t_0, \varphi)$, $k = 1, 2, \ldots$. Then $y^k(t)$ solves the following initial value problem

$$\begin{cases} \dot{y}^k(t) = f(t_k + t, y^k_t), \\ y^k_0 = x^f_{t_k}(t_0, \varphi). \end{cases}$$

Because of the relative compactness of $\{x^f_t(t_0, \varphi); t \geq t_0\}$ and the precompactness of f with respect to U, without loss of generality, we may assume that $x^f_{t_k}(t_0, \varphi) \to \psi \in U$ and $f(t_k + t, \xi) \to g(t, \xi)$ as $k \to \infty$ for $(t, \xi) \in [0, \infty) \times U$, where $g : [0, \infty) \times U \to R^n$ is continuous. Therefore, by the regularity of f and the well-known continuous dependence of a solution on its initial data and the right-hand side functional of the equation, we obtain that $\lim_{t \to \infty} y^k(t) = x^g(t; 0, \psi)$ uniformly on any compact set in $[0, \infty)$. Let k be sufficiently large such that $t_k \geq T(\varepsilon)$. Then $\|y^k_t - \widehat{K}\| = \|x^f_{t_k + t}(t_0, \phi) - \widehat{K}\| \geq \delta(\varepsilon)$ for $t \geq 0$ from which it follows that $\|x^g_t(0, \psi) - \widehat{K}\| \geq \delta(\varepsilon)$ for $t \in [0, \infty)$, contradicting the assumption (i).

Therefore $\lim_{t \to \infty} x^f_t(t_0, \varphi) = \widehat{K}$. This completes the proof.

We now apply Theorem 4.1 to system (4.4) and obtain

THEOREM 4.2. For any solution of (4.4) with $M_2(\theta) \geq 0$ for $\theta \in [-\tau, 0]$, we have $\lim_{t \to \infty} M_2(t) = M_2^*$.

Proof. For any solution $M_1(t)$ of system (4.2), let $f : [0, \infty) \times C([-\tau, 0], R) \to R$ be defined by

$$f(t, \psi) = -\beta_2 \psi^2(0) + b_{22}\alpha_2 \psi(-\tau) - D_{12}\psi(0) + D_{12}M_1(t) + b_{21}\alpha_1 M_1(t - \tau)$$

for $(t, \psi) \in [0, \infty) \times C([-\tau, 0], R)$. It is easy to prove, in a similar way to the proof of Theorem 3.1, that for any $\varphi \in C_1^+$ and $t_0 \geq 0$, the solution of (4.4) with $M_{20} = \varphi$ (denoted by $M_2^f(t_0, \varphi)$) and the solution of (4.3) with $m_{20} = \varphi$ (denoted by $M_2^g(t_0, \varphi)$) satisfy that $M_{2t}^f(t_0, \varphi), M_{2t}^g(t_0, \varphi) \in C_1^+$ for $t \geq t_0$, where $g : C([-\tau, 0], R) \to R$ is defined by

$$g(\psi) = -\beta_2 \psi^2(0) + b_{22}\alpha_2 \psi(-\tau) - D_{12}\psi(0) + (D_{12} + b_{21}\alpha_1)\frac{e^{\gamma_1 \tau}\alpha_1}{\beta_1}$$

for $\psi \in C([-\tau, 0], R)$.

Evidently, f is positively precompact and regular with respect to C_1^+, and $H(f) = \{g\}$. Using a similar argument to that in Sec. 3, we can prove that for any $(t_0, \varphi) \in [0, \infty) \times C_1^+$, $\lim_{t \to \infty} M_{2t}^g(t_0, \varphi) = \widehat{M}_2^*$.

We now prove that $\widehat{M}_2^*$ is eventually uniformly stable with respect to system (4.4) and C_1^+. Since $\widehat{M}_2^*$ is globally uniformly asymptotically stable with respect to system (4.3), by the well-known inverse theorem of Liapunov direct method (see, e.g., [43]), there exist a constant $\delta_0 > 0$ and a continuous functional $V(\varphi)$ defined for $\varphi \in C_1^+$ with $\|\varphi - \widehat{M}_2^*\| \leq \delta_0$, a constant $L > 0$ and increasing continuous functions $\alpha, \beta, \gamma : [0, \infty) \to [0, \infty)$ with $\alpha(0) = \beta(0) = \gamma(0) = 0$ such that

$$\alpha(\|\varphi - \widehat{M}_2^*\|) \leq V(\varphi) \leq \beta(\|\varphi - \widehat{M}_2^*\|),$$

$$|V(\varphi) - V(\psi)| \leq L\|\varphi - \psi\|,$$

$$\frac{d}{dt}V(M_{2t}^g(t_0, \varphi)) \leq -\gamma(\|M_{2t}^g(t_0, \varphi) - \widehat{M}_2^*\|)$$

for all $\varphi, \psi \in C_1^+$ with $\|\varphi - \widehat{M}_2^*\| \leq \delta_0$ and $\|\psi - \widehat{M}_2^*\| \leq \delta_0$. Therefore

$$\frac{d}{dt}V(M_{2t}^f(t_0, \varphi)) \leq -\gamma(\|M_{2t}^f(t_0, \varphi) - \widehat{M}_2^*\|) + L(D_{12} + b_{21}\alpha_1)\left\|M_{1t} - \frac{e^{-\gamma\tau}\alpha_1}{\beta_1}\right\|.$$

For any $\varepsilon > 0$, there exists $\delta(\varepsilon) > 0$ and $T(\varepsilon) > 0$ such that $\beta(\delta(\varepsilon)) < \alpha(\varepsilon)$ and $L(D_{12} + b_{21}\alpha_1)\|M_{1t} - (\alpha_1\hat{e}^{-\gamma_1\tau})/\beta_1\| \leq \gamma(\delta(\varepsilon))$ for $t \geq t_0 + T(\varepsilon)$. If at an instant $t^* \geq t_0 + T(\varepsilon)$, $\|M_{2t^*}^f(t_0, \varphi) - \widehat{M}_2^*\| < \delta(\varepsilon)$, then we claim that $\|M_{2t}^f(t_0, \varphi) - \widehat{M}_2^*\| < \varepsilon$ for $t \geq t^*$. Otherwise, there exists $t_2 > t_1 \geq t^*$ such that $\|M_{2t_1}^f(t_0, \varphi) - \widehat{M}_2^*\| = \delta(\varepsilon)$, $\|M_{2t_2}^f(t_0, \varphi) - \widehat{M}_2^*\| = \varepsilon$ and $\delta(\varepsilon) \leq \|M_{2t}^f(t_0, \phi) - \widehat{M}_2^*\| \leq \varepsilon$ for $t \in [t_1, t_2]$. Therefore on $[t_1, t_2]$, we have

$$\frac{d}{dt}V(M_{2t}^f(t_0, \varepsilon)) = -\gamma(\delta(\varepsilon)) + L(D_{12} + b_{21}\alpha_1)\left\|M_{1t} - \frac{\alpha_1\hat{e}^{-\gamma_1\tau}}{\beta_1}\right\| \leq 0$$

from which it follows that

$$\alpha(\varepsilon) = \alpha(\|M_{2t_2}^f(t_0, \varphi) - \widehat{M}_2^*\|) \leq V(M_{2t_2}^f(t_0, \varphi))$$

$$\leq V(M_{2t_1}^f(t_0, \varphi)) \leq \beta(\|M_{2t_1}^f(t_0, \varphi) - \widehat{M}_2^*\|) \leq \beta(\delta(\varepsilon))$$

which is contrary to $\beta(\delta(\varepsilon)) < \alpha(\varepsilon)$.

Therefore by Theorem 4.1, $\lim_{t \to \infty} M_{2t}^f(t_0, \varphi) = \widehat{M}_2^*$ for all $t_0 \geq 0$ and $\varphi \in C_1^+$. This proves the theorem.

Hence, we have shown the global asymptotic stability of the positive equilibrium for mature populations. It is easy to establish the global convergence of immature populations.

5. Convergence in the case of nonsymmetric dispersal: a general multi-patch environment. In this section, we briefly indicate how the approaches employed in the previous sections can be effectively combined to study the global asymptotic stability of a positive equilibrium state in a more general nonsymmetric dispersion

situation where the environment is assumed to consist of several groups (denoted by $G_1, G_2, \ldots, G_m$) of patches such that in each group the patches are connected by dispersal and there further exists dispersal from patches in the group G_k to the patches in groups G_p, $k \le p \le m$, but there exists no dispersal from the patches in groups G_p, $k \le p \le m$, to the patches in group G_k, where $k = 1, \ldots, m$.

To derive a model equation, we suppose that the group G_k, $1 \le k \le m$, consists of patches $P_{k1}, \ldots, P_{kn_k}$. The following notations will be used throughout this section.

γ_{kj}: the death rate of the immature population in the patch P_{kj};

α_{kj}: the birth rate into the immature population in the patch P_{kj};

β_{kj}: the death rate of the mature population in the patch P_{kj};

I_{kj}: the immature population in the patch P_{kj};

M_{kj}: the mature population in the patch P_{kj};

$x_{kj}(s, t - \tau)$: the growth rate at the instant s, $t - \tau \le s \le t$, of the immature population in the patch P_{kj} born at the instant $t - \tau$, where $1 \le k \le m$ and $1 \le j \le n_k$;

δ_{kjh}: the dispersal coefficient of immature population from the patch P_{kh} to P_{kj};

D_{kjh}: the dispersal coefficient of mature population from the patch P_{kh} to P_{kj}, where $1 \le k \le m$, $1 \le j \ne h \le n_k$;

δ_{kj}^{qr}: the dispersal coefficient of the immature population from the patch P_{qr} to the patch P_{kj};

D_{kj}^{qr}: the dispersal coefficient of the mature population from the patch P_{qr} to the patch P_{kj}, where $2 \le k \le m$, $1 \le j \le n_k$, $1 \le q < k$, $1 \le r \le n_q$.

Then based on the same argument as in Sec. 2, we have the following model equation

$$\frac{d}{dt}I_{kj}(t) = -\gamma_{kj}I_{kj}(t) + \alpha_{kj}M_{kj}(t) - x_{kj}(t, t - \tau)$$
$$+ \sum_{h \ne j}\delta_{kjh}[I_{kh}(t) - I_{kj}(t)] + \sum_{\substack{q < k \\ 1 \le r \le n_q}}\delta_{kj}^{qr}[I_{qr}(t) - I_{kj}(t)],$$

$$\frac{d}{dt}M_{kj}(t) = -\beta_{kj}M_{kj}^2(t) + x_{kj}(t, t - \tau)$$
$$+ \sum_{h \ne j}D_{kjh}[M_{kh}(t) - M_{kj}(t)] + \sum_{\substack{q < k \\ 1 \le r \le n_q}}D_{kj}^{qr}[M_{qr}(t) - M_{kj}(t)],$$

$$\frac{\partial}{\partial s}y_{kj}(s, t - \tau) = x_{kj}(s, t - \tau), \qquad x_{kj}(t - \tau, t - \tau) = \alpha_{kj}M_{kj}(t - \tau),$$

$$\frac{\partial}{\partial s}y_{kj}(s, t - \tau) = -\gamma_{kj}y_{kj}(s, t - \tau) + \sum_{h \ne j}\delta_{kjh}[y_{kh}(s, t - \tau) - y_{kj}(s, t - \tau)]$$
$$+ \sum_{\substack{q < k \\ 1 \le r \le n_q}}\delta_{kj}^{qr}[y_{qr}(s, t - \tau) - y_{kj}(s, t - \tau)], \tag{5.1}$$

where $t - \tau \le s \le t$, $1 \le k \le m$, $1 \le j \le n_k$.

To simplify the above model, we introduce the following notations:

$$I_k(t) = (I_{k1}(t), \ldots, I_{kn_k}(t))^T,$$

$$M_k(t) = (M_{k1}(t), \ldots, M_{kn_k}(t))^T,$$

$$x_k(s, t - \tau) = (x_{k1}(s, t - \tau), \ldots, x_{kn_k}(s, t - \tau))^T,$$

$$y_k(s, t - \tau) = (y_{k1}(s, t - \tau), \ldots, y_{kn_k}(s, t - \tau))^T,$$

$$\alpha_k M_k(t) = (\alpha_{k1} M_{k1}(t), \ldots, a_{kn_k} M_{kn_k}(t))^T,$$

$$\beta_k M_k^2(t) = (\beta_{k1} M_{k1}^2(t), \ldots, \beta_{kn_k} M_{kn_k}^2(t))^T,$$

$$\Delta_k = (\delta_{kjh})_{1 \leq j, h \leq n_k} \quad \text{with } \delta_{kjj} = 0, \, 1 \leq j \leq n_k,$$

$$D_k = (D_{kjh})_{1 \leq j, h \leq n_k} \quad \text{with } D_{kjj} = 0, \, 1 \leq j \leq n_k,$$

$$\Gamma_k = \text{diag} \left(\gamma_{kj} + \sum_{h \neq j} \delta_{kjh} + \sum_{\substack{q < k \\ 1 \leq r \leq n_q}} \delta_{kj}^{qr} \right)_{1 \leq j \leq n_k},$$

$$L_k = \text{diag} \left(\sum_{h \neq j} D_{kjh} + \sum_{\substack{q < k \\ 1 \leq r \leq n_q}} D_{kj}^{qr} \right)_{1 \leq j \leq n_k},$$

$$\Delta_{kq} = (\delta_{kj}^{qr})_{\substack{1 \leq j \leq n_k \\ 1 \leq r \leq n_q}},$$

$$D_{kq} = (D_{kj}^{qr})_{\substack{1 \leq j \leq n_k \\ 1 \leq r \leq n_q}},$$

where $1 \leq k \leq m$. Then the model equation can be rewritten in the following vector form

$$\frac{d}{dt} I_k(t) = -\Gamma_k I_k(t) + \alpha_k M_k(t) - x_k(t, t - \tau) + \Delta_k I_k(t) + \sum_{q < k} \Delta_{kq} I_q(t),$$

$$\frac{d}{dt} M_k(t) = -\beta_k M_k^2(t) + x_k(t, t - \tau) + D_k M_k(t) - L_k M_k(t) + \sum_{q < k} D_{kq} M_q(t),$$

$$x_k(t - \tau, t - \tau) = \alpha_k M_k(t - \tau),$$

$$\frac{\partial}{\partial s} y_k(s, t - \tau) n = x_k(s, t - \tau), \qquad t - \tau \leq s \leq t,$$

$$\frac{\partial}{\partial s} y_k(s, t - \tau) = -\Gamma_k y_k(s, t - \tau) + \Delta_k y_k(s, t - \tau) + \sum_{q < k} \Delta_{kq} y_q(s, t - \tau).$$

(5.2)

Let

$$A = \begin{pmatrix} -\Gamma_1 + \Delta_1 & 0 & \cdots & 0 \\ \Delta_{21} & -\Gamma_2 + \Delta_2 & \cdots & 0 \\ & \cdots & & \\ \Delta_{m1} & \Delta_{m2} & \cdots & -\Gamma_m + \Delta_m \end{pmatrix}.$$

By the assumption that patches in the same group are connected by dispersion, Δ_k and D_k are irreducible matrix for $1 \leq k \leq m$. This implies that $-\Gamma_k + \Delta_k$ is an irreducible matrix for $1 \leq k \leq m$, and thus $B_{kk} = e^{(-\Gamma_k + \Delta_k)\tau}$ is a positive matrix for $1 \leq k \leq m$.

Using the same approach as in Sec. 2, we obtain the following formula

$$
\begin{pmatrix} x_1(t, t-\tau) \\ \vdots \\ x_m(t, t-\tau) \end{pmatrix} = \begin{pmatrix} B_{11} & 0 & \cdots & 0 \\ B_{21} & B_{22} & \cdots & 0 \\ & \cdots & \cdots & \\ B_{m1} & B_{m2} & \cdots & B_{mm} \end{pmatrix} \begin{pmatrix} \alpha_1 M_1(t-\tau) \\ \vdots \\ \alpha_m M_m(t-\tau) \end{pmatrix} \tag{5.3}
$$

where

$$
\begin{pmatrix} B_{11} & 0 & \cdots & 0 \\ B_{21} & B_{22} & \cdots & \cdots \\ & \cdots & \cdots & \\ B_{m1} & B_{m2} & \cdots & B_{mm} \end{pmatrix} = e^{A\tau}.
$$

Because the off diagonal elements of A are nonnegative, each B_{ij}, $1 \leq j \leq i \leq m$, is nonnegative.

Substituting formula (5.3) into system (5.2), we get the following simplified model equation

$$
\begin{aligned}
\frac{dI_k(t)}{dt} &= -\Gamma_k I_k(t) + \alpha_k M_k(t) + \Delta_k I_k(t) + \sum_{q<k} \Delta_{kq} I_q(t) \\
&\quad - \sum_{q \leq k} B_{kq} \alpha_q M_q(t-\tau), \\
\frac{dM_k(t)}{dt} &= -B_k M_k^2(t) + B_{kk} \alpha_k M_k(t-\tau) - L_k M_k(t) + D_k M_k(t) \\
&\quad + \sum_{q<k} B_{kq} \alpha_q M_q(t-\tau) + \sum_{q<k} D_{kq} M_q(t),
\end{aligned} \tag{5.4}
$$

where $1 \leq k \leq m$.

The first equation for the mature population turns out to be

$$
\frac{dM_1(t)}{dt} = -\beta_1 M_1^2(t) - L_1 M_1(t) + B_{11} \alpha_1 M_1(t-\tau) + D_1 M_1(t). \tag{5.5}
$$

Since B_{11} is a positive matrix and D_1 is irreducible, we can use the approach in Sec. 3 to prove that there exists a unique positive vector M_1^* in R^{n_1} such that $\lim_{t \to \infty} M_1(t) = M_1^*$ if $M_1(\theta) \geq 0$ for $\theta \in [-\tau, 0]$ and $M_1 \not\equiv 0$ on $[-\tau, 0]$.

Therefore, the system

$$
\begin{aligned}
\frac{dm_2(t)}{dt} &= -\beta_2 m_2^2(t) + B_{22} \alpha_2 m_2(t-\tau) - L_2 m_2(t) + D_2 m_2(t) \\
&\quad + B_{21} \alpha_1 M_1^* + D_{21} M_1^*
\end{aligned} \tag{5.6}
$$

is a limiting equation of the second equation for the mature population

$$
\begin{aligned}
\frac{dM_2(t)}{dt} &= -\beta_2 M_2^2(t) + B_{22} \alpha_2 M_2(t-\tau) - L_2 M_2(t) + D_2 M_2(t) \\
&\quad + B_{21} \alpha_1 M_1(t-\tau) + D_{21} M_1(t).
\end{aligned} \tag{5.7}
$$

Using the same argument used in Sec. 3, we can prove that there exists a positive vector M_2^* in R^{n_2} such that $\lim_{t \to \infty} m_2(t) = M_2^*$ if $m_2(\theta) \geq 0$ for $\theta \in [-\tau, 0]$. Therefore, employing the argument of Sec. 4, we can prove that $\lim_{t \to \infty} M_2(t) = M_2^*$ provided $M_2(\theta) \geq 0$ for $\theta \in [-\tau, 0]$.

Repeating the above argument for a finite number of steps (m), we obtain that there exists a positive vector $(M_1^*, \dots, M_m^*) \in R^{n_1 + \dots + n_m}$ such that

$$\lim_{t \to \infty} (M_1(t), \dots, M_m(t)) = (M_1^*, \dots, M_m^*)$$

if $M_i(\theta) \geq 0$ for $\theta \in [-\gamma, 0]$ and $i = 1, \dots, m$ and $M_1 \not\equiv 0$ on $[-\tau, 0]$.

Finally, using the same argument as for Theorem 3.3, we obtain the following global convergence theorem.

THEOREM 5.1. There exists a positive vector $(M_1^*, \dots, M_m^*) \in R^{n_1 + \dots + n_m}$ such that if

(i) $M_k(\theta) \geq 0$ for $\theta \in [-\tau, 0]$ and $k = 1, \dots, m$, $M_1 \neq 0$ on $[-\tau, 0]$,

(ii) $\begin{pmatrix} I_1(0) \\ \vdots \\ I_m(0) \end{pmatrix} \geq \int_{-\tau}^0 e^{-As} \begin{pmatrix} \alpha_1 M_1(\theta) \\ \vdots \\ \alpha_m M_m(\theta) \end{pmatrix} d\theta$,

then

$$\lim_{t \to \infty} (M_1(t), \dots, M_m(t)) = (M_1^*, \dots, M_m^*),$$

$$\lim_{t \to \infty} (I_1(t), \dots, I_m(t)) = A^{-1}(e^{A\tau} - I) \begin{pmatrix} \alpha_1 M_1^* \\ \vdots \\ \alpha_m M_m^* \end{pmatrix}.$$

REMARK 5.1. The above model can be thought of as describing stage structured population dispersal in a patchy environment where each patch is subdivided into subpatches.

REMARK 5.2. It would be interesting to consider the competition of the mature and immature individuals for resources. We wish to investigate such a competition in a further paper.

REFERENCES

[1] W. G. Aiello and H. I. Freedman, *A time-delay model of single-species growth with stage structure*, Math. Biosci. **101**, 139–153 (1990)

[2] F. S. Anderson, *Competition in populations of one age group*, Biometrica **16**, 19–27 (1960)

[3] Z. Artstein, *Uniform asymptotic stability via the limiting equations*, J. Differential Equations **27**, 172–189 (1978)

[4] H. J. Barclay and P. Van den Driessche, *A model for a species with two life history stages and added mortality*, Ecol. Model **11**, 157–166 (1980)

[5] E. Beretta, F. Solimano, and Y. Takeuchi, *Global stability and periodic orbits for two-patch predator-prey diffusion-delay models*, Math. Biosci. **85**, 153–183 (1987)

[6] E. Beretta and Y. Takeuchi, *Global stability of single-species diffusion models with continuous time delays*, Bull. Math. Biol. **49**, 431–448 (1987)

[7] G. J. Butler, H. I. Freedman, and P. Waltman, *Uniformly persistent systems*, Proc. Amer. Math. Soc. **96**, 425–430 (1986)

[8] G. J. Butler and P. Waltman, *Persistence in dynamical systems*, J. Differential Equations **63**, 255–263 (1986)

[9] H. I. Freedman, *Single species migration in two habitats: persistence and extinction*, Math. Model **8**, 778–780 (1987)

[10] H. I. Freedman, *Persistence and extinction in models of two-habitat migration*, Math. Comput. Modelling **12** 105–112 (1989)

[11] H. I. Freedman, B. Rai, and P. Waltman, *Mathematical models of population interactions with dispersal II: differential survival in a change of habitat*, J. Math. Anal. Appl. **115**, 140–154 (1986)

[12] H. I. Freedman, J. B. Shukla, and Y. Takeuchi, *Population diffusion in a two-patch environment*, Math. Biosci. **95**, 111–123 (1989)

[13] H. I. Freedman and Y. Takeuchi, *Global stability and predator dynamics in a model of prey dispersal in a patchy environment*, Nonlinear Anal. **13**, 993–1002 (1989)

[14] H. I. Freedman and Y. Takeuchi, *Predator survival versus extinction as a function of dispersal in a predator-prey model with patchy environment*, Appl. Anal. **31**, 247–266 (1989)

[15] H. I. Freedman and P. Waltman, *Mathematical models of population interaction with dispersal I: Stability of two habitats with and without a predator*, SIAM J. Appl. Math. **32**, 631–648 (1977)

[16] H. I. Freedman and J. H. Wu, *Steady state analysis in a model for population diffusion in a multi-patch environment*, preprint

[17] W. S. C. Gurney and R. M. Nisbet, *Fluctuating periodicity, generation separation, and the expression of larval competition*, Theor. Pop. Biol. **28**, 150–180 (1985)

[18] W. S. C. Gurney, R. M. Nisbet, and J. H. Lawton, *The systematic formulation of tractable single species population models incorporating age structure*, J. Animal Ecol. **52**, 479–495 (1983)

[19] J. R. Haddock, T. Krisztin, and J. H. Wu, *Asymptotic equivalence of neutral equations and retarded equations with infinite delay*, Nonlinear Anal. **14**, 369–377 (1990)

[20] J. R. Haddock and J. Terjeki, *Liapunov-Razumikhin functions and invariance principle for functional differential equations*, J. Differential Equations **48**, 95–122 (1983)

[21] J. K. Hale, *Theory of functional Differential Equations*, Springer-Verlag, New York, 1979

[22] J. K. Hale, *Asymptotic Behavior of Dissipative Systems*, Mathematical Surveys and Monographs, Vol. 25, Amer. Math. Soc., Providence, 1988

[23] H. Hastings, *Dynamics of a single species in a spatially varying environment: the stabilizing role of high dispersal rates*, J. Math. Biol. **16**, 49–55 (1982)

[24] M. W. Hirsch, *The dynamical systems approach to differential equations*, Bull. Amer. Math. Soc. **11**, 1–64 (1984)

[25] R. D. Holt, *Population dynamics in two patch environment: some anomalous consequences of optional habitat selection*, Theor. Pop. Biol. **28**, 181–208 (1985)

[26] Yu. S. Koslesov, *Properties of solutions of a class of equations with lag which describe the dynamics of change in the population of a species with the age structure taken into account*, Math. USSR Sb. **45**, 91–100 (1983)

[27] V. Lakshmikantham and S. Leela, *Differential and Integral Inequalities*, Vol. 2, Academic Press, New York, 1969

[28] H. D. Landahl and B. D. Hanson, *A three stage population model with cannibalism*, Bull. Math. Biol. **37**, 11–17 (1975)

[29] S. A. Levin, *Dispersion and population interactions*, Am. Nat. **108**, 207–228 (1974)

[30] R. H. Martin and H. L. Smith, *Reaction-diffusion systems with time delays: monotonicity invariance, comparison and convergence*, preprint

[31] S. W. Pacala and J. Roughgarden, *Spatial heterogeneity and interspecific competition*, Theor. Pop. Biol. **21**, 92–113 (1982)

[32] G. R. Sell, *Nonautonomous differential equations and topological dynamics, I. The basic theory*, Trans. Amer. Math. Soc. **127**, 241–262 (1967)

[33] G. R. Sell, *Nonautonomous differential equations and topological dynamics, II. Limiting equations*, Trans. Amer. Math. Soc. **127**, 263–283 (1967)

[34] N. Shigesada and J. Roughgarden, *The role of rapid dispersal in the population dynamics of competition*, Theor. Pop. Biol. **21**, 353–372 (1982)

[35] J. G. Skellam, *Random dispersal in theoretical populations*, Biometrika **38**, 196–218 (1951)

[36] H. L. Smith, *Monotone semiflows generated by functional differential equations*, J. Differential Equations **66**, 420–442 (1987)

[37] Y. Takeuchi, *Global stability in generalized Lotka-Volterra diffusion systems*, J. Math. Anal. Appl. **116**, 209–221 (1986)

[38] Y. Takeuchi, *Diffusion effect on stability of Lotka-Volterra models*, Bull. Math. Biol. **48**, 585–601 (1986)

[39] R. R. Vance, *The effect of dispersal on population stability in one-species, discrete-space population growth models*, Am. Nat. **123**, 230–254 (1984)

[40] G. F. Webb, *Theory of Nonlinear Age-Dependent Population Dynamics*, Marcel Dekker, New York, 1985

[41] S. N. Wood, S. P. Blythe, S. C. Gurney, and R. M. Nisbet, *Instability in mortality estimation schemes related to stage-structure population models*, IMA J. Math. Appl. Med. Biol. **6**, 47–68 (1989)

[42] T. Yoshizawa, *Stability Theory by Liapunov's Second Method*, Publications of the Mathematical Society of Japan, No. 9, The Mathematical Society of Japan, Tokyo, 1966