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HETEROCLINIC ORBITS AND CONVERGENCE OF ORDER-PRESERVING SET-CONDENSING SEMIFLOWS WITH APPLICATIONS TO INTEGRODIFFERENTIAL EQUATIONS

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ABSTRACT. Several theorems on order-preserving set-condensing semiflows are proved. These results are then applied to a model of stage-structured populations with dispersal between patches in a heterogeneous environment.

1. Introduction. In [**15**], Smith proved that a cooperative and irreducible retarded functional differential equation with finite delay generates an eventually strongly monotone semiflow to which the powerful theory of monotone dynamical systems developed by Hirsch [**5, 6**] and Matano [**7, 8**] as well as the spectral theory of positive operators established by Nussbaum [**10, 11**] can be applied. Results in [**15**] have later been extended to more general retarded or neutral equations with finite delay [**16, 20**] and some integrodifferential equations with certain specific kernels [**18, 19**]. However, as an example in [**18**] indicates, solutions of integrodifferential equations with general kernels which satisfy the usual quasimonotonicity and irreducibility conditions always coincide with their initial values, and hence the solution semiflows can never be (eventually) strongly monotone if the state space consisting of some functions defined on the noncompact interval $(-\infty, 0]$ is endowed with the natural pointwise ordering. It is therefore natural to ask to what extent Smith's results can be generalized to cooperative and irreducible integrodifferential equations with general kernels and, more generally, to what extent the strong monotonicity or strong order-preserving conditions in the theory of monotone dynamical systems due to Hirsch and Matano can be relaxed.

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One of the main purposes of this paper is to provide a partial solution to the above questions by establishing the existence of monotone heteroclinic orbits connecting two order related equilibria and the convergence of bounded orbits for semiflows generated by cooperative and irreducible integrodifferential equations. Our approach is based on the observation that a cooperative and irreducible integrodifferential equation generates an order-preserving and set-condensing semiflow $\{\Phi_t\}_{t\geq 0}$ on an ordered Banach space X with order cone P, which satisfies the following property. There exists a Banach space $X_0 \subseteq X$ with an order cone P_0 such that for every equilibrium $x_0 \in X_0$ and every compact invariant subset $Y \subseteq X$, if $x_0 <_P Y$ then there exists $y_0 \in X_0$ so that $x_0 \ll_{P_0} y_0 <_P Y$. X_0 is commonly the space of constant mappings which can be identified with Euclidean space. A semiflow satisfying the above property is said to be *quasi strongly order-preserving* (QSOP). In vague terms, a QSOP semiflow separates an equilibrium and a compact invariant subset which are order related. It will be demonstrated that a strongly order-preserving semiflow must be QSOP, but the converse is not necessarily true.

We will show that (i) for an order-preserving and set-condensing semiflow, if x_1 and x_2 are two ordered equilibria and there are no other equilibria between x_1 and x_2, then there exists an entire monotone heteroclinic orbit connecting x_1 and x_2; (ii) for a set-condensing and QSOP semiflow, if every equilibrium is stable, then each bounded orbit is convergent to a single equilibrium. These types of results have been obtained by Hirsch [**6**], Matano [**8**], Poláčik [**12, 13**], Takáč [**17**], Smith [**14**], Alikakos, Hess and Matano [**1**], and Dancer and Hess [**2**] for order-compact and strongly order-preserving semiflows. Our proof indicates that after certain modifications, the argument of Dancer and Hess [**2**] based on Nussbaum's fixed point index theory [**9**] applies to more general set-condensing and QSOP semiflows as well.

Our general results will be illustrated by the following stage-structured model

$$\dot{I}_i(t) = -\gamma_i I_i(t) + \sum_{j\neq i} \delta_{ji}[I_j(t) - I_i(t)] + \alpha_i M_i(t) - \sum_{j=1}^{n} \alpha_j \int_{-\infty}^{t} b_{ij}(t-s) M_j(s)\, ds \tag{4.1}$$

$$\dot{M}_i(t) = -\beta_i M_i^2(t) + \sum_{j\neq i} D_{ji}[M_j(t) - M_i(t)] + \sum_{j=1}^{n} \alpha_j \int_{-\infty}^{t} b_{ij}(t-s) M_j(s)\, ds$$

for the growth of a single-species population dispersing in an environment consisting of n patches, where $I_i(t)$ and $M_i(t)$ represent the immature and mature population densities, respectively, in the ith patch, and $b_{ij} : [0,\infty) \to [0,\infty)$ denotes the probability distribution of the maturation period, $1 \le i,\, j \le n$. When the maturation period is identical to a constant, the global attractivity of a unique positive equilibrium is proved in [**3**]. We will show that this result is still valid even if there is some spread of the maturation period around the mean value in which the kernel functions are general distribution functions.

2. Heteroclinic orbits and convergence for quasi strongly order-preserving semiflows. Let E be an ordered Banach space with order cone P. For $u, v \in E$ we write $u \ge v$ if $u - v \in P$, $u > v$ if $u - v \in P\backslash\{0\}$, and $u \gg v$ if P has nonempty interior and $u - v \in \operatorname{int} P$. We will sometimes use $\le_P$ to denote the order induced by the cone P.

Assume that U is a subset of E, and $S : U \to U$ is a continuous, strictly order-preserving mapping (i.e., $u > v$ implies $S(u) > S(v)$). We say that $x \in U$ is a subsolution for the fixed point equation $S(u) = u$ provided $x \le S(x)$; x is a strict subsolution if $x < S(x)$. Similarly, a (strict) supersolution y is defined by $S(y) \le y$, $(S(y) < y)$. An entire orbit is a sequence $\{z_n; n \in \mathbf{Z}\}$ in U such that $z_{n+1} = S(z_n)$ for all n.

Theorem 2.1. *Let $u_1 < u_2$ be order related fixed points of S, and let*

$$X := [u_1, u_2]_E = \{x \in E; u_1 \le x \le u_2\}.$$

Assume $X \subseteq U$ and $S : X \to X$ is a set-condensing mapping with respect to a measure μ of noncompactness. Then either

(a) *there exists a further fixed point u of S such that $u_1 < u < u_2$, or*

(b) *there exists an entire orbit of strict subsolutions $\{x_n : n \in \mathbf{Z}\}$ connecting u_1 and u_2, i.e., $x_{n+1} = S(x_n)$ and $x_{n+1} > x_n$ for all n, $x_n \to u_1$ as $n \to -\infty$ and $x_n \to u_2$ as $n \to \infty$, or*

(c) *there exists an entire orbit of strict supersolutions* $\{y_n : n \in \mathbf{Z}\}$ *connecting* u_2 *and* u_1, *i.e.,* $y_{n+1} = S(y_n)$, $y_{n+1} < y_n$ *for all* n, $y_n \to u_1$ *as* $n \to +\infty$ *and* $y_n \to u_2$ *as* $n \to -\infty$.

The above theorem represents a considerable improvement on corresponding results obtained by Hirsch [**6**], Matano [**8**], Poláčik [**13**], Takáč [**17**] and Smith [**14**]. This improvement was achieved by Dancer and Hess [**2**] under the assumption that $S(X)$ is relatively compact in E. Our results show that the relative compactness of $S(X)$ can be replaced by the set-condenseness of $S : X \to X$. The main idea of the following proof belongs to Dancer and Hess. We thus focus on the modification of their argument for a set-condensing mapping S.

Proof. Consider $X = [u_1, u_2]_E$ as a metric space with induced metric and assume that there are no fixed points in X except u_1 and u_2. Following the argument of Dancer and Hess [**2**], we can show that either there exists a strict supersolution u_ε on $\partial B_X(u_2, \varepsilon)$ for every sufficiently small $\varepsilon > 0$, or there exists a strict subsolution u_ε on $\partial B_X(u_1, \varepsilon)$ for every sufficiently small $\varepsilon > 0$, where $B_X(a, \varepsilon) = \{x \in X : ||x - a|| < \varepsilon\}$ for every $a \in X$ and $\varepsilon > 0$. We take the latter case and assume, without loss of generality that $u_1 = 0$. Let $\delta_0 > 0$ be small enough so that $u_2 \notin B_X(u_1, \delta_0)$. By continuity of S at $u_1 = 0$, there exists a sequence of real numbers

$$\delta_0 > \delta_1 > \delta_2 > \delta_3 > \cdots \to 0$$

and a sequence of strict subsolutions $\{u_k\}_{k=1}^{\infty} \subseteq X$ such that

$$||v_k|| = \delta_k, \qquad S(B_X(0, \delta_{k+1})) \subseteq B_X(0, \delta_k)$$

for all $k = 0, 1, \dots$. Let

$$A = \{S^n(v_k) : k = 1, 2, \dots, n = 0, 1, \dots\}.$$

Then

$$A = S(A) \cup \{v_1, v_2, \dots\}. \tag{4.1}$$

Note that $v_k \to u_1 = 0$ as $k \to \infty$. We have

$$\mu(\{v_1, v_2, \dots\}) = 0$$

from which by (4.1) it follows that $\mu(A) = \mu(S(A))$. So the set-condensedness of S implies that $\mu(A) = 0$. Thus A is relatively compact in X. The remaining part of the proof is identical to that of [**2**]; that is, first of all, since for every $k \geq 1$ we have

$$0 < v_k < S(v_k) < S^2(v_k) \cdots \to u_2,$$

we can find $n(k) \geq k - 1$ such that $w_k := S^{n(k)}(v_k)$ satisfies $\delta_1 \leq ||w_k|| \leq \delta_0$. Due to the relative compactness of A, there exists a subsequence $\{w_{k'}\}$ converging in X to x_0, and a subsequence of $\{S^{n(k')-1}(v_{k'})\}$ converging in X to x_1 and so forth. Consequently, we can get an entire orbit $\{x_n : n \in \mathbf{Z}\}$ consisting of subsolutions such that $x_n \to u_1$ as $n \to -\infty$ and $x_n \to u_2$ as $n \to \infty$. This completes the proof. □

By a standard limiting argument, Theorem 2.1 implies a corresponding result for continuous-time dynamical systems.

Corollary 2.2. *Let $\Phi : R_+ \times U \to U$ be a semiflow satisfying*

(i) $\Phi(t, u) < \Phi(t, v)$ *for* $t \geq 0$, *if* $u < v$.

(ii) *for any* $t_0 > 0$, $\Phi(t_0, \cdot) : U \to U$ *is set-condensing with respect to* μ.

Suppose $u_1 < u_2$ are order related equilibria of Φ and $X := [u_1, u_2]_E$ contains no equilibria in X except u_1 and u_2. Then there exists a monotone heteroclinic orbit connecting u_1 and u_2.

In what follows, we assume that $\Phi : R_+ \times U \to U$ is a given semiflow satisfying assumptions (i) and (ii) of Corollary 2.2.

Definition 2.3. Φ is said to be *quasi strongly order-preserving* (QSOP) if for every sequence $\{y^p\}$ of equilibria and every compact invariant subset $A \subseteq U$ such that

$$\lim_{p \to \infty} y^p = y < A, \qquad y < y^p \quad \text{for } p = 1, 2, \dots,$$

there exists an integer p_0 such that $y < y^{p_0} \leq A$.

Proposition 2.4. *If Φ is strongly order-preserving (i.e., P has nonempty interior and $u < v$ implies $\Phi(t,u) \ll \Phi(t,v)$ for $t > 0$), then Φ is* QSOP.

Proof. Assume that $\{y^p\}$ is a sequence of equilibria of Φ and A is an invariant compact subset such that $\lim_{p\to\infty} y^p = y < A$ and $y < y^p$ for every $p = 1, 2, \dots$. For a fixed $\tau > 0$ and given $a \in A$ there exists $a^* \in A$ such that $a = \Phi(\tau, a^*)$. Since $y < a^*$, by the strongly order-preserving property of Φ, $y \ll a$. So, from the compactness of A, there exists a neighborhood O of y such that $y \in O \ll A$. On the other hand, since $y^p \to y$ as $p \to \infty$ there exists p_0 so that $y^{p_0} \in O$. Therefore, $y < y^{p_0} \leq A$. This completes the proof. □

Proposition 2.5. *Suppose that there exists an ordered Banach space E_0 whose order cone P_0 has nonempty interior such that*

(i) *every equilibrium of Φ belongs to E_0;*

(ii) *$E_0 \subseteq E$; the norm-topology of E_0 is weaker than the induced topology from E; and for every $a, b \in E_0$, $a \leq_{P_0} b$ if and only if $a \leq_P b$;*

(iii) *for every $y \in E_0$ and an invariant compact subset $A \subset E$ such that $y <_P A$ there exists $y_0 \in E_0$ such that $y \ll_{P_0} y_0 \leq_P A$.*

Then Φ is QSOP.

Proof. Suppose that $\{y^p\}$ is a sequence of equilibria of Φ and A an invariant compact subset such that $\lim_{p\to\infty} y^p = y < A$ and $y < y^p$ for $p = 1, 2, \dots$. By assumptions (iii) there exists $y_0 \in E_0$ so that $y \ll_{P_0} y_0 \leq_P A$. On the other hand, since $y^p \to y$ in E and the norm-topology of E_0 is weaker than the induced topology from E, we have $y^p \to y$ in E_0 according to assumption (i) of Proposition 2.5. So there exists an integer p_0 so that $y^{p_0} \ll_{P_0} y_0$. From the last part of assumption (ii), we get

$$y <_P y^{p_0} \leq_P y_0 \leq A.$$

This completes the proof. □

Remark 2.6. In the next section we will show that a semiflow generated by an integrodifferential equation satisfying certain quasimonotonicity conditions and irreducibility conditions satisfies all conditions of Proposition 2.5, but is not strongly order-preserving.

Theorem 2.6. *Suppose that* Φ *is* QSOP, $a \in U$ *is a subsolution* (*i.e.,* $a \le \Phi(t,a)$ *for* $t > 0$) *and* $b \in U$ *is a supersolution* (*i.e.,* $b \ge \Phi(t,b)$ *for* $t > 0$) *such that* $a < b$ *and* $V := [a,b]_E \subseteq U$. *Assume that all equilibria of* Φ *in* V *are stable with respect to* V (*i.e., for every equilibrium* $u \in V$ *and every* $\varepsilon > 0$ *there exists* $\delta > 0$ *such that* $\Phi(t, B_V(u,\delta)) \subseteq \Phi_V(u,\varepsilon)$ *for all* $t \ge 0$). *Then every bounded positive semiorbit in* V *converges, i.e., for every* $v \in V$ *such that* $\{\Phi(t,v)\}_{t\ge 0}$ *is bounded, there exists an equilibrium* $e(v)$ *so that* $\lim_{t\to\infty}\Phi(t,v) = e(v)$.

The above result can be proved by a similar argument to that of Theorem 2 in [**2**], and thus the proof is omitted.

3. Applications to functional differential equations with infinite delays. In this section we prove that solution semiflows of certain retarded functional differential equations with infinite delay are QSOP. In order not to hide the main idea behind technical details, we will state our results for functional differential equations defined in the phase space C_α, but our results can easily be generalized to equations defined in general phase spaces satisfying the fundamental algebraic, topological and ordering axioms formulated in [**19**, Axioms 1–12].

Let $\alpha > 0$ be a given constant. Define

$$C_\alpha = \{\varphi : (-\infty, 0) \to \mathbf{R}^n \text{ is continuous; } \lim_{s\to-\infty} |\varphi(s)|e^{\alpha s} \text{ exists}\}.$$

Then C_α is a Banach space with the norm

$$||\varphi||_\alpha = \sup_{s\le 0} |\varphi(s)|e^{\alpha s} \quad \text{for } \varphi \in C_\alpha.$$

Moreover, C_α has the following property. If $x : R \to R^n$ is continuous and $x_0 \in C_\alpha$, then $x_t \in C_\alpha$ for $t \ge 0$ and the mapping $t \in [0,\infty) \to x_t \in C_\alpha$ is continuous, where $x_t(\theta) = x(t+\theta)$ for $\theta \le 0$.

We consider the following retarded functional differential equations with infinite delay

$$\dot{x}(t) = f(x_t) \tag{3.1}$$

where $f : C_\alpha \to R^n$ is completely continuous and satisfies a local Lipschitz condition. It has been shown (see, cf. [**4**]) that for any $\varphi \in C_\alpha$, (3.1) has a unique solution, denoted by $x(t,\varphi)$, satisfying the initial condition $x_0 = \varphi$. Moreover, if $x(t;\varphi)$ is noncontinuable on $(-\infty, b)$ with $b < \infty$, then $\lim_{t\to b^-} ||x_t(\varphi)||_\alpha = \infty$.

In what follows, we assume that for every $\varphi \in C_\alpha$, $x_t(\varphi)$ is defined for all $t \geq 0$. Let $\Phi : R_+ \times C_\alpha \to C_\alpha$ be defined by

$$\Phi(t,\varphi) = x_t(\varphi), \qquad t \geq 0, \quad \varphi \in C_\alpha.$$

Then Φ is a semiflow on C_α. Let $S(t) : C_\alpha \to C_\alpha$ denote the translation operator, i.e.,

$$S(t)\varphi(\theta) = \begin{cases} \varphi(0), & \text{if } \theta \in [-t, 0] \\ \varphi(t+\theta), & \text{if } \theta \in (-\infty, -t) \end{cases}$$

for $\varphi \in C_\alpha$. Define $S_0(t) = S(t)|_{C_\alpha^0}$, where

$$C_\alpha^0 = \{\varphi \in C_\alpha; \varphi(0) = 0\}.$$

Then

$$||S_0(t)|| \leq e^{\alpha t} < 1 \quad \text{if } t > 0.$$

Therefore, by Theorems 2.2 and 2.3 in [**19**], $\Phi(t,0) : C_\alpha \to C_\alpha$ is set-contractive with respect to the Kuratowskii measure of noncompactness for every $t > 0$, and the ω-limit set, $\omega(\varphi)$, of any bounded solution $\{x_t(\varphi)\}_{t\geq 0}$ is nonempty, compact, connected and invariant.

C_α is also an ordered Banach space with the order cone C_α^+ defined by

$$C_\alpha^+ = \{\varphi \in C_\alpha; \varphi(\theta) \geq_{R_+^n} 0 \text{ for } \theta \leq 0\}.$$

Clearly, $\varphi \leq_{C_\alpha^+} \psi$ implies that $\varphi(0) \leq_{R_+^n} \psi(0)$. Moreover, if $x, y : R \to R^n$ are given continuous functions such that $x_0, y_0 \in C_\alpha$, $x_0 \leq_{C_\alpha^+} y_0$ and $x(t) \leq_{R_+^n} y(t)$ for $t \geq 0$, then $x_t \leq_{C_\alpha^+} y_t$ for $t \geq 0$. Therefore, by Theorem 2.6 of [**19**], the solution semiflow $\Phi : R_+ \times C_\alpha \to C_\alpha$ is strictly order-preserving if f satisfies the following "quasimonotonicity" condition (QM):

$$f_i(\varphi) \leq f_i(\psi) \quad \text{if } \varphi, \psi \in C_\alpha, \varphi \leq_{C_\alpha^+} \psi \quad \text{and} \quad \varphi_i(0) = \psi_i(0).$$

To obtain the quasi-strongly order-preserving property of Φ, we need the following one-sided Lipschitz condition, an ignition condition and an irreducibility condition of the vector field f:

(LI). There exists a functional $h : C_\alpha \times C_\alpha \to R$ such that $f_i(\psi) - f_i(\varphi) \geq h(\varphi, \psi)[\psi_i(0) - \varphi_i(0)]$ for all $i = 1, \dots, n$, provided that $\varphi \leq_{C_\alpha^+} \psi$.

(IG). There exists $t_1 > 0$ such that for any continuous functions $x, y : R \to R^n$ with $x_0 <_{C_\alpha^+} y_0$ and $x(t) = y(t)$ for $t \in (0, t_1]$ there exists $k \in \{1, \dots, n\}$ such that $\sup\{f_k(y_t) - f_k(x_t); 0 \leq t \leq t_1\} > 0$.

(IR). There exists a constant $t_2 > 0$ such that if Σ is a proper, nonempty subset of $\{1, \dots, n\}$, $\tau > t_2$ and $x, y : R \to R^n$ are given continuous functions such that

(i) $x_j(t) < y_j(t)$ for all $j \in \Sigma$ and $t \in [\tau - t_2, \tau]$;

(ii) $x_j(t) = y_j(t)$ for all $j \in \Sigma^C$ and $t \in [\tau - t_2, \tau]$;

(iii) $x_t \leq_{C_\alpha^+} y_t$ for $t \in [0, \tau - t_2]$;

then there exists a $k \in \Sigma^C$ such that $f_k(y_\tau) - f_k(x_\tau) > 0$.

Theorem 3.1. *If f satisfies* (QM), (LI), (IG) *and* (IR), *then the solution semiflow $\Phi : R_+ \times C_\alpha \to C_\alpha$ defined by* (3.1) *is set-contractive, strictly order-preserving and quasi-strongly order-preserving.*

Proof. Employing the same argument as that of Theorem 2.7 of [**19**], we can show that if $\varphi <_{C_\alpha^+} \psi$, then $x_i(t, \varphi) < x_i(t, \psi)$ for all $i = 1, \dots, n$ and all $t > t_1 + (n-1)t_2$.

Let E_0 denote the space of all constant mappings from $(-\infty, 0]$ into R^n. E_0 can be identified with R^n with the natural positive cone $P_0 = R^n_+$. Clearly, every equilibrium of Φ belongs to E_0, the Euclidean norm of E_0 is weaker than the induced topology from C_α, and for any $x, y \in E_0$ we have $x \leq_{R^n_+} y$ if and only if $x \leq_{C_\alpha^+} y$.

Suppose $y \in E_0$ and A is a given compact invariant set such that $y < A$.

Claim 1. $y = y(t) \ll_{R^n_+} \varphi(t)$ *for every $\varphi \in A$ and $t \leq 0$.*

In fact, if this claim is not true then there exists $t^* \leq 0$, an integer

$m \in \{1, \dots, n\}$ and $\varphi \in A$ such that

$$y_m = y_m(t^*) = \varphi_m(t^*).$$

Let $\tau = 1 + t_1 + (n-1)t_2 - t^*$. Since A is invariant, there exists $\varphi^* \in A$ such that $\varphi = x_\tau(\varphi^*)$. So

$$x(\tau + t^*, \varphi^*) = (x_\tau(\varphi^*))(t^*) = \varphi(t^*).$$

On the other hand, since $y < \varphi^*$, from the first part of our proof it follows that

$$y_m = x_m(\tau + t^*; y) < x_m(\tau + t^*; \varphi^*) = \varphi_m(t^*),$$

a contradiction to $y_m = \varphi_m(t^*)$.

Claim 2. *Let J denote the vector in R^n with each component* 1. *Then there exists $\delta > 0$ such that*

$$y + \delta J \leq_{R^n_+} \varphi(t)$$

for every $t \leq 0$ and $\varphi \in A$.

By way of contradiction, if this claim is false, then there exists a sequence of real numbers $\{t_k\} \subseteq (-\infty, 0]$ such that

$$y + \frac{1}{k} J \not\leq_{R^n_+} \varphi(t_k),$$

so there must be an integer $l \in \{1, \dots, n\}$ such that

$$y_l + \frac{1}{k} J \geq \varphi_l(t_k) \tag{3.2}$$

for infinitely many k. Note that $\varphi_{t_k} \in A$ and A is compact. So there exists a subsequence, denoted by $\{\varphi_{t_k}\}$ for simplicity, such that $\varphi_{t_k} \to \psi \in A$ as $k \to \infty$ for some $\psi \in A$. Therefore, $\varphi_{t_k}(0) \to \psi(0)$ in R^n. That is, $\varphi(t_k) \to \psi(0)$ in R^n. Taking the limit as $k \to \infty$ in (3.2), we get $y_l \geq \psi_l(0)$, a contradiction to Claim 1.

Let $y_0 = y + (\delta/2)J$. Then $y_0 \in E_0$ and $y \ll_{R^n_+} y_0 \leq_{C^+_\alpha} A$. This completes the proof by Proposition 2.5. □

Applying Theorem 2.6 to retarded equation (3.1), we get the following result.

Theorem 3.2. *Suppose that $U \subseteq C_\alpha$ is a subset invariant with respect to the semiflow Φ generated by equation* (3.1)*.*

(i) *Assume that f satisfies* (QM)*. If $\varphi <_{C_\alpha^+} \psi$ are order related equilibria of Φ and $X := [\varphi, \psi]_{C_\alpha}$ contains no equilibria of Φ except φ and ψ, then there exists a monotone heteroclinic orbit connecting φ and ψ.*

(ii) *Assume that f satisfies* (QM), (LI), (IG) *and* (IR)*. If $\varphi \in U$ is a subsolution and $\psi \in U$ is a supersolution with $\varphi <_{C_\alpha^+} \psi$ and $V := [\varphi, \psi]_{C_\alpha} \subseteq U$, and if every equilibrium of Φ in V is stable with respect to V, then every solution in V converges.*

4. An application to stage-structured population growth models. In [**3**] a system of retarded functional differential equations was 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 global stability of a unique positive equilibrium is proved by using a convergence theorem of Hirsch [**6**] for strongly monotone semiflows, under the assumption that the length of time from birth to maturity is a constant which is uniform for each individual in all patches. However, in real situations there is bound to be some spread of the maturation period about the mean value. Therefore, the proposed model in [**3**] is only a crude approximation, and a distributed delay should be used to allow for stochastic elements in the maturation process. The purpose of this section is to apply our results in previous sections in order to establish a global stability result for the unique positive equilibrium of a model incorporating stochastic elements in the maturation process.

Suppose that the system is composed of n patches connected by dispersal 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, $i = 1, \dots, n$. 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 $\alpha_i > 0$.

(H2). The death rate of the immature population in the ith patch is proportional to the existing immature population with proportionality constant $\gamma_i > 0$.

(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 $\beta_i > 0$.

(H4). 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 $\delta_{ji} \geq 0$ for $i \neq j$. Moreover, the dispersal matrices $D = (D_{ij})$ and $\Delta = (\delta_{ij})$, where $\delta_{ii} = D_{ii} = 0$ for $i = 1, \dots, n$, are irreducible.

(H5). The probability distribution of the maturation period in the ith patch is a bounded continuous function $p_i : [0, \infty) \to [0, \infty)$ with $\int_0^\infty p_i(s)\, ds = 1$ and $p_i(s) > 0$ for all $s \geq \tau_i$, where $\tau_i \geq 0$ is a constant.

Under the above assumptions, we obtain the following model equations

$$
\begin{aligned}
\frac{d}{dt} I_i(t) &= -\gamma_i I_i(t) + \sum_{j \neq i} \delta_{ji}[I_j(t) - I_i(t)] + \alpha_i M_i(t) \\
&\quad - \int_{-\infty}^{t} x_i(t,s) p_i(t-s)\, ds \\
\frac{d}{dt} M_i(t) &= -\beta_i M_i^2(t) + \sum_{j \neq i} D_{ji}[M_j(t) - M_i(t)] \\
&\quad + \int_{-\infty}^{t} x_i(t,s) p_i(t-s)\, ds
\end{aligned} \tag{4.1}
$$

where $1 \leq i \leq n$, $x_i(t,s)$, $-\infty < s \leq t$, denotes the growth rate at the instant t of the immature population in the ith patch born at the instant $s \leq t$. Obviously,

$$
x_i(t,t) = \alpha_i M_i(t). \tag{4.2}
$$

To derive an explicit formula for $x_i(t,s)$ in terms of $I_i(t)$ and $M_i(t)$, we denote by $y_i(t,s)$ the concentration of the immature population in the ith patch born at the instant $s \le t$. Then

$$\partial y_i(t,s)/\partial t = x_i(t,s), \qquad -\infty < s \le t \tag{4.3}$$

and

$$\frac{\partial}{\partial t} y_i(t,s) = -\gamma_i y_i(t,s) + \sum_{j\neq i} \delta_{ji}[y_j(t,s) - y_i(t,s)]. \tag{4.4}$$

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

$$a_{ij} = \begin{cases} \delta_{ji}, & \text{if } i \neq j \\ -\gamma_i - \sum_{j\neq i} \delta_{ji}, & \text{if } i = j. \end{cases}$$

Then (4.4) can be solved with respect to t,

$$y(t,s) = e^{A(t-s)} y(s,s), \tag{4.5}$$

where

$$y(t,s) = (y_1(t,s), \ldots, y_n(t,s))^T, \qquad s \le t.$$

So

$$\frac{\partial}{\partial t} y(t,s) = A e^{A(t-s)} y(s,s), \qquad s \le t. \tag{4.6}$$

Substituting (4.2) and (4.3) into (4.6), we get

$$(\alpha_1 M_1(t), \ldots, \alpha_n M_n(t))^T = A y(t,t) \tag{4.7}$$

from which it follows by (4.6) and (4.7) that

$$(x_1(t,s), \ldots, x_n(t,s))^T = e^{A(t-s)} (\alpha_1 M_1(s), \ldots, \alpha_n M_n(s))^T. \tag{4.8}$$

Substituting this equality into the second equation of (4.1), we obtain the following system of integrodifferential equations

$$\begin{aligned} \frac{d}{dt} M_i(t) = -\beta_i M_i^2(t) + \sum_{j\neq i} D_{ji}[M_j(t) - M_i(t)] \\ + \sum_{j=1}^{n} \int_{-\infty}^{t} p_i(t-s) b_{ij}(t-s) \alpha_j M_j(s)\, ds, \end{aligned} \tag{4.9}$$

$1 \le i \le n$, where $e^{At} = (b_{ij}(t))$.

Remark 4.1. Substituting (4.8) into the first equation of (4.1), we can get

$$\begin{aligned}(I_1(t), \dots, I_n(t))^T = e^{At}\Big[&(I_1(0), \dots, I_n(0))^T \\ &- \int_{-\infty}^0 e^{-As} \int_0^t \operatorname{diag}(p_1(\theta-s), \dots, p_n(\theta-s))\, d\theta \\ &\qquad \cdot (\alpha_1 M_1(s), \dots, \alpha_n M_n(s))^T\, ds\Big] \\ &+ \int_0^t e^{A(t-s)} \int_{t-s}^\infty \operatorname{diag}(p_1(\xi), \dots, p_n(\xi))\, d\xi \\ &\qquad \cdot (\alpha_1 M_1(s), \dots, \alpha_n M_n(s))^T\, ds.\end{aligned}$$

Therefore, if $e^{At} \to 0$ and $M_i(t) \to M_i^*$ as $t \to \infty$ for $i = 1, \dots, n$, then

$$\begin{aligned}&(I_1(t), \dots, I_n(t))^T \\ &\quad \to \int_0^\infty e^{Au} \int_u^\infty \operatorname{diag}(p_1(\xi), \dots, p_n(\xi))\, d\xi (\alpha_1 M_1^*, \dots, \alpha_n M_n^*)\, du\end{aligned}$$

as $t \to \infty$. Consequently, in what follows we will concentrate on (4.9) only.

Note that $a_{ij} \ge 0$, if $i \ne j$, $\sum_{j=1}^n a_{ij} = -\gamma_i < 0$ for $i = 1, \dots, n$. So every element of e^{At} is positive for all $t > 0$ and $e^{At} \to 0$ as $t \to \infty$. This implies that there exist constants $N > 0$ and $\alpha > 0$ such that

$$0 < b_{ij}(t) \le Me^{-\alpha t} \tag{4.10}$$

for all $t > 0$ and all $i, j = 1, \dots, n$.

Let $F = (F_1, \dots, F_n)^T : C_\alpha \to R^n$ be given by

$$\begin{aligned}F_i(\varphi) = -\beta_i \varphi_i^2(0) &+ \sum_{j \ne i} D_{ji}[\varphi_j(0) - \varphi_i(0)] \\ &+ \sum_{j=1}^n \int_{-\infty}^0 p_i(-\theta) b_{ij}(-\theta) \alpha_j \varphi_j(\theta)\, d\theta\end{aligned}$$

for $\varphi \in C_\alpha$ and $i = 1, \ldots, n$. Because each $\int_0^\infty p_i(s)\,ds = \infty$ and b_{ij} satisfies (4.10), F is completely continuous. It can be easily verified that F satisfies (QM), (LI), (IG) and (IR) with $t_1 = t_2 = \max_{1\le i\le n} \tau_i \ge 0$. Consequently, the solution semiflow of (4.9) is strictly order-preserving and quasi-strongly order-preserving.

Let $M(t,\varphi) = (M_1(t,\varphi), \ldots, M_n(t,\varphi))^T$ be the unique solution of (4.9) with $\varphi \in C_\alpha^+$. Clearly, $M(t,0) = 0$ for all $t \ge 0$. So, by the order-preserving property, C_α^+ is positively invariant with respect to the solution semiflow. That is, $\varphi \in C_\alpha^+$ implies that $M(t,\varphi) \ge_{R_+^n} 0$ for all $t \ge 0$.

Lemma 4.2. *Let J denote the vector in R^n with each component* 1*. If $\varepsilon > 0$ is sufficiently small, then $\widehat{\varepsilon J}$ is a subsolution of the solution semiflow defined by equation* (4.9)*, where for every $x \in R^n$, $\hat{x} \in C_\alpha$ denotes the constant mapping with the value x.*

Proof. Let $M(t) = M(t, \widehat{\varepsilon J})$. If there exists $t^* \ge 0$ and an integer i such that $M_i(t^*) = \varepsilon$ and $M(t) \ge_{R_+^n} \varepsilon J$ for all $t \in [0, t^*]$, then

$$\begin{aligned}\dot{M}_i(t^*) &\ge -\beta_i \varepsilon^2 + \sum_{j=1}^n \int_{-\infty}^{t^*} p_i(t^*-s) b_{ij}(t^*-s)\alpha_j \varepsilon\, ds \\ &= \Big[-\beta_i\varepsilon + \sum_{j=1}^n \alpha_j \int_0^\infty p_i(\theta) b_{ij}(\theta)\,d\theta\Big]\varepsilon \\ &> 0,\end{aligned}$$

provided

$$\varepsilon < \min_{1\le i\le n} \beta_i^{-1} \sum_{j=1}^n \alpha_j \int_0^\infty p_i(\theta) b_{ij}(\theta)\,ds.$$

Therefore, $M_i(t) \ge \varepsilon$ for all $t \ge 0$ and $i = 1, \ldots, n$. This completes the proof. □

Similarly, we can prove

Lemma 4.3. *If $N > 0$ is a constant such that*

$$N > \max_{1\le i\le n} \beta_i^{-1} \sum_{j=1}^{N} \alpha_j \int_0^\infty p_i(\theta) b_{ij}(\theta)\, d\theta, \tag{4.11}$$

then $\widehat{NJ}$ is a supersolution of the solution semiflow defined by equation (4.9).

We now are in the position to state the main result of this section.

Theorem 4.4. *Assume* (H1)–(H5) *are satisfied. Then equation* (4.9) *has a unique positive equilibrium $\hat{q}$. Moreover, we have*:

(i) *If $\varphi \in C_\alpha^+ \backslash \{0\}$ is given so that $\sup_{\substack{1\le i\le n\\ \theta\le 0}} \varphi_i(\theta) < \infty$, then* $\lim_{t\to\infty} M(t,\varphi) = q$.

(ii) *There exists a monotone heteroclinic orbit connecting* 0 *and* $\hat{q}$.

Proof. (ii) is an immediate consequence of Theorem 3.2 since F satisfies (QM), (LI), (IG) and (IR). To prove (i), we notice that system (4.9) has exactly the same set of equilibria as that for the following system of ordinary differential equations

$$\dot{z}_i = -\beta_i z_i^2 + \sum_{j\ne i} D_{ji}(z_j - z_i) + \sum_{j=1}^{n} \alpha_j \int_0^\infty p_i(\theta) b_{ij}(\theta)\, d\theta z_j, \tag{4.12}$$

$1 \le i \le n$. It can easily be shown that all solutions of (4.12) are bounded and the zero solution of (4.12) is not a global attractor. So, by the theorem of Hirsch [**5**, Theorem 6.1], system (4.12) has a unique equilibrium $q \in \operatorname{int} R_+^n$ such that every solution of (4.12) in $R_+^n|\{0\}$ is convergent to q.

Consequently, $\hat{q}$ is a unique equilibrium in $C_\alpha^+|\{0\}$ of (4.9). Moreover, since q is asymptotically stable as an equilibrium of (4.12), by Theorem 3.2 of [**19**], $\hat{q}$ is asymptotically stable as an equilibrium of (4.9).

For any $\varphi \in C_\alpha^+|\{0\}$ with

$$0 < \inf_{\substack{1\le i\le n\\ \theta\le 0}} \varphi_i(\theta) \le \sup_{\substack{1\le i\le n\\ \theta\le 0}} \varphi_i(\theta) < \infty,$$

there exists $\varepsilon > 0$ and $N > 0$ such that $\widehat{\varepsilon J}$ is a subsolution and $\widehat{NJ}$ is a supersolution of (4.9), $\widehat{\varepsilon J} \leq \varphi \leq \widehat{NJ}$, and $\hat{q}$ is the only equilibrium in $[\widehat{\varepsilon J}, \widehat{NJ}]_{C_\alpha}$. So applying Theorem 3.2 to $[\widehat{\varepsilon J}, \widehat{NJ}]_{C_\alpha}$, we have $\lim_{t\to\infty} M(t,\varphi) = \hat{q}$.

It remains to prove that $\lim_{t\to\infty} M(t,\varphi) = \hat{q}$ for all $\varphi \in C_\alpha^+|\{0\}$ with $\sup_{\substack{1\leq i\leq n\\ \theta\leq 0}} \varphi_i(\theta) < \infty$ and $\inf_{\substack{1\leq i\leq n\\ \theta\leq 0}} \varphi_i(\theta) = 0$. From the first part of the proof of Theorem 3.1, $M_i(t,\varphi) > 0$ for all $i = 1, \dots, n$ and all $t > \tau^* := n \max_{1\leq i\leq n} \tau_i$. Choose $T > \tau^*$ sufficiently large so that

$$\sum_{j=1}^n \alpha_j \int_0^{T-\tau^*-1} p_i(\theta) b_{ij}(\theta)\, d\theta \geq \frac{1}{2} \sum_{j=1}^n \alpha_j \int_0^\infty p_i(\theta) b_{ij}(\theta)\, d\theta.$$

Since $M_i(t,\varphi) > 0$ for all $i = 1, \dots, n$ and for $t > \tau^*$, there exists $\varepsilon^* > 0$ such that

$$M_i(t,\varphi) \geq \varepsilon^* \qquad \text{for } i = 1, \dots, n, \quad t \in [\tau^* + 1, T].$$

Without loss of generality, we may assume that

$$\varepsilon^* < \min_{1\leq i\leq n} \frac{1}{2\beta_i} \sum_{j=1}^n \alpha_j \int_0^\infty p_i(\theta) b_{ij}(\theta)\, d\theta.$$

We now prove that $M_i(t,\theta) \geq \varepsilon^*$ for $i = 1, \dots, n$, and for all $t > T$. By way of contradiction, if this is not true, then there exists $t^* > T$ and an integer $i \in \{1, \dots, n\}$ so that $M_i(t^*;\varphi) = \varepsilon^*$ and $M_j(t;\varphi) \geq \varepsilon^*$ for all $t \in [\tau^* + 1, t^*]$ and all $j = 1, \dots, n$. So $\dot{M}_i(t^*;\varphi) \leq 0$, but

$$\begin{aligned}
\dot{M}_i(t^*;\varphi) &\geq -\beta_i {\varepsilon^*}^2 + \sum_{j=1}^n \alpha_j \int_{-\infty}^{t^*} p_i(t^*-s) b_{ij}(t^*-s) M_j(s;\varphi)\, ds \\
&\geq \Big[-\beta_i \varepsilon^* + \sum_{j=1}^n \alpha_j \int_{\tau^*+1}^{t^*} p_i(t^*-s) b_{ij}(t^*-s)\, ds \Big] \varepsilon^* \\
&= \Big[-\beta_i \varepsilon^* + \sum_{j=1}^n \alpha_j \int_0^{t^*-(\tau^*+1)} p_i(\theta) b_{ij}(\theta)\, d\theta \Big] \varepsilon^* \\
&\geq \Big[-\beta_i \varepsilon^* + \sum_{j=1}^n \alpha_j \int_0^{T-(\tau^*+1)} p_i(\theta) b_{ij}(\theta)\, d\theta \Big] \varepsilon^*
\end{aligned}$$

$$\geq \left[-\beta_i\varepsilon^* + \frac{1}{2}\sum_{j=1}^{n} \alpha_j \int_0^\infty p_i(\theta) b_{ij}(\theta)\, d\theta \right] \varepsilon^*$$
$$\geq 0,$$

a contradiction.

Fix $\psi \in \omega(\varphi)$. Since $M_i(t,\varphi) > \varepsilon^*$ for all $t \geq \tau^* + 1$, we have $\inf_{\substack{1\leq i\leq n \\ \theta\leq 0}} \psi_i(\theta) \geq \varepsilon^*$. Therefore, $\lim_{t\to\infty} M(t;\psi) = q$. Note that $\hat{q}$ is stable. So for any $\varepsilon > 0$ there exists $\delta > 0$ such that if $\xi \in C_\alpha$ and $||\xi - \hat{q}||_\alpha < \delta$ then $||M_t(\xi) - \hat{q}||_\alpha < \varepsilon$ for all $t \geq 0$. For this chosen $\delta > 0$, since $\lim_{t\to\infty} M_t(\psi) = \hat{q}$, there exists $T^* > 0$ so that $||M_{T^*}(\psi) - \hat{q}||_\alpha < \delta$. On the other hand, since $\psi \in \omega(\varphi)$, there exists a sequence $t_k \to \infty$ such that $M_{t_k}(\varphi) \to \psi$ as $k \to \infty$. By the continuity of solutions of (4.9) on initial data, $M_{t_k+T^*}(\varphi) \to M_{T^*}(\psi)$ as $k \to \infty$. Therefore there exists $K > 0$ such that $||M_{t_K+T^*}(\varphi) - \hat{q}||_\alpha M < \delta$. This implies that $||M_t(\varphi) - \hat{q}||_\alpha < \varepsilon$ for all $t \geq t_K + T^*$, that is, $\lim_{t\to\infty} M_t(\varphi) = \hat{q}$. This completes the proof. □

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