Stability results for a nonlinear two-species competition model with size-structure

LIU Yan[1]   HE Ze-rong[2]

Abstract. We formulate a system of integro-differential equations to model the dynamics of competition in a two-species community, in which the mortality, fertility and growth are size-dependent. Existence and uniqueness of nonnegative solutions to the system are analyzed. The existence of the stationary size distributions is discussed, and the linear stability is investigated by means of the semigroup theory of operators and the characteristic equation technique. Some sufficient conditions for asymptotical stability / instability of steady states are obtained. The resulting conclusion extends some existing results involving age-independent and age-dependent population models.

§1   Introduction

Body size is manifestly one of the most important physical attributes of an individual. It is such a factor that determines an individual's energetic requirements and ability to exploit resources. It has an important effect on the nature of an individual's interaction with the physical environment and other biological species, including competitors, predators and co-operators. Since the development of the first size-structured population model, the classical Sinko-Streifer model [1], many researchers have focused their attention on this subject, and many relevant models, including both single-species models and multi-species ones, have been investigated(e.g.,[2-25]).

Here, we briefly review a few of existing results. In [2] a model for the growth of a size-structured cell population reproducing by fission into two identical daughters was formulated and analyzed. Using semigroup theory and compactness arguments the authors established the existence of a stable size distribution under certain conditions. In [4], the authors presented and studied a general nonlinear model for populations in which individuals were characterized by chronological age and an arbitrary finite number of additional structure variables. Therein,

the existence of unique solutions and of equilibria to the model were proved, and the local asymptotic stability of equilibria was discussed too. In [5] a size-structured population model with a nonlinear growth rate depending on the individual's size and the total population was developed. The authors demonstrated the well-posedness of the model, investigated the asymptotic behaviors of the solutions, and also discussed sufficient stability conditions to a stationary distribution when the total population tended to a constant. In [6], the authors formulated numerical schemes for the size-structured population models, and analyzed optimal rates of convergence. In [8, 9] a general model of size-dependent population dynamics with nonlinear growth rate was studied. Using Schauder's fixed point theorem, the author proved the existence of a local solution and established the uniqueness and continuous dependence on initial data. They also discussed the positivity of the solutions and global existence as well as L^∞ solutions. In [10] a quasi-linear hierarchical size-structured model with nonlinear growth, mortality and reproduction rates was established. The authors developed a numerical scheme, proved its convergence and presented two examples. In [13] the authors investigated a nonlinear size-structured population dynamical model. The linear stability and instability results under biologically meaningful conditions from the vital rates were derived. In [16] population models incorporating age, size, and spatial structures were analyzed by means of semigroups theory. The author gave an illustration of such structure in a situation of tumor growth.

However, considerably less work has been done for size-structured multi-species models because of the complexity. In [19] a discrete-time, size-structured model of m competing species in a chemostat was studied. The authors showed that the competitive exclusion principle is valid for their model and the winner is the population that is able to grow at the lowest nutrient concentration. In [21] the authors discussed a quasi-linear size-structured population model, in which the vital rate of each subpopulation depends on the total population due to competition. They provided conditions from the vital rates guaranteeing competitive exclusion under the closed reproduction, while under the open reproduction they showed that all ecotypes coexist for all times.

In this paper, we formulate a nonlinear size-structured two-species population model, which is in the form of integro-partial differential equations. The remainder of our paper is organized as follows. In Section 2, we present the basic model and state some assumptions. In Section 3, we demonstrate the existence and uniqueness of the solutions to the model, and also discuss the existence of the stationary size distributions. In Section 4, we linearize the nonlinear system and derive some regularity properties for the simplified system by means of the semigroups theory [26], after deduce the characteristic equation and present some conditions for stability and instability of the equlibria in section 5. The final section contains some remarks.

§2   The basic model

We propose the following model to describe the dynamics of a two-species competition system with size-structure ($i = 1, 2$):

$$\frac{\partial p_i(s,t)}{\partial t} + \frac{\partial(g_i(s, P_1(t), P_2(t))p_i(s,t))}{\partial s} = -\mu_i(s, P_1(t), P_2(t))p_i(s,t) \ , s \in [0, m], \ t > 0, \quad (2.1)$$

$$g_i(0, P_1(t), P_2(t))p_i(0, t) = \int_0^m \beta_i(s, P_1(t), P_2(t))p_i(s, t)\mathrm{d}s \ , \ t > 0, \tag{2.2}$$

$$p_i(s, 0) = p_{i0}(s) \ , \ s > 0, \tag{2.3}$$

where $p_i(s, t)$ denotes the size-specific density of individuals in the ith population at the moment t; $P_i(t) = \int_0^m p_i(s, t)\mathrm{d}s$ is the total population size at time t of the ith population; m denotes the maximum size of both two populations; The functions $\mu_i(s, P_1(t), P_2(t))$, $\beta_i(s, P_1(t), P_2(t))$ and $g_i(s, P_1(t), P_2(t))$ denote mortality, fertility and growth rate of the ith population, respectively, which incorporating interspecific and intraspecific interactions; $p_{i0}(s)$ represents the initial size distribution of the ith population.

The following assumptions will be used throughout this paper ($i = 1, 2$):

(A1): $\mu_i(\cdot, P_1, P_2) \in C^1([0, m] \times (0, \infty) \times (0, \infty))$. $\mu_i \geq \mu_i^* > 0$, μ_i^* is a positive constant. μ_i is a nonnegative Lipschitzian function on $[0, m] \times (0, \infty) \times (0, \infty)$ with constant L_{μ_i}.

(A2): $\beta_i(\cdot, P_1, P_2) \in C^1([0, m] \times (0, \infty) \times (0, \infty))$, $0 \leq \beta_i \leq \beta_i^*$, β_i^* is a positive constant. β_i is a nonnegative Lipschitzian function on $[0, m] \times (0, \infty) \times (0, \infty)$ with constant L_{β_i}.

(A3): $g_i(\cdot, P_1, P_2) \in C^2([0, m] \times (0, \infty) \times (0, \infty))$ with $g_i(m, \cdot, \cdot) = 0$. g_i is a strictly positive Lipschitzian function on $[0, m) \times (0, \infty) \times (0, \infty)$ with constant L_{g_i}.

(A4): p_{i0} is a nonnegative continuous function, and $p_{i0} \in L^1(0, m)$.

Definition 2.1 A integrable nonnegative function pair $(p_1(s, t), p_2(s, t))$ on Q_m is a solution of the basic system (2.1)-(2.3) if $P_i(t), i = 1, 2$, are continuous functions on $(0, \infty)$ and $p_i(s, t)$ satisfy (2.2), (2.3) and

$$Dp_i(s, t) = -\tilde{\mu}_i(s, P_1(t), P_2(t))p_i(s, t), \ (s, t) \in Q_m := [0, m] \times (0, \infty), \tag{2.4}$$

with

$$Dp_i(s, t) = \lim_{h \to 0} \frac{p_i(\varphi_i(t+h; t, s), t+h) - p_i(s, t)}{h}$$

where

$$\tilde{\mu}_i(s, P_1(t), P_2(t)) = \mu_i(s, P_1(t), P_2(t)) + \frac{\partial(g_i(s, P_1(t), P_2(t)))}{\partial s}$$

and $\varphi_i(t; t_0, s_0)$ is the solution of the differential equation

$$s'(t) = g_i(s(t), P_1(t), P_2(t))$$

with initial condition $s(t_0) = s_0$.

It is obvious that $\varphi_i(t; t_0, s_0)$ satisfies the integral equation

$$\varphi_i(t; t_0, s_0) = s_0 + \int_{t_0}^t g_i(\varphi_i(x; t_0, s_0), P_1(x), P_2(x))dx. \tag{2.5}$$

Let $z_i(t) := \varphi_i(t; 0, 0)$ denote the characteristic curve through the origin $(0, 0)$ in the (s, t)-plane.

Now we state a property of the characteristic curves defined by (2.5), which is essential for the following discussion.

Lemma 2.2 Let $s = \varphi_i(t; \tau, \xi)$, $i = 1, 2$. Then we have that s is differentiable with respect to τ and ξ, respectively, and

$$\frac{ds}{d\tau} = -g_i(\xi, P_1(\tau), P_2(\tau))e^{\int_\tau^t \partial_s g_i(\varphi_i(x; \tau, \xi), P_1(x), P_2(x))dx},$$

$$\frac{ds}{d\xi} = e^{\int_\tau^t \partial_s g_i(\varphi_i(x; \tau, \xi), P_1(x), P_2(x))dx}.$$

The proof is essentially the same as that of Lemma 3.1 in [21], and hence is omitted.

§3   Existence and uniqueness

In the spirit of [5], we use the fixed point theorem to discuss the existence and uniqueness of solutions of the basic model (2.1)-(2.3). By the method of characteristics, we reduce this problem to a system of coupled equations for $P_i(t)$ and $B_i(t)$, here $B_i(t) := \int_0^m \beta_i(s, P_1(t), P_2(t)) p_i (s,t) \mathrm{d}s$.

Integrating (2.4) along the characteristics, we obtain $(i = 1, 2)$

$$p_i(s,t) = \begin{cases} \dfrac{B_i(\tau)}{g_i(0, P_1(\tau), P_2(\tau))} e^{-\int_\tau^t \tilde{\mu}_i(\varphi_i(x;\tau,0), P_1(x), P_2(x))dx}, & s < z_i(t), \\ p_{i0}(\varphi_i(0;t,s)) e^{-\int_0^t \tilde{\mu}_i(\varphi_i(x;t,s), P_1(x), P_2(x))dx}, & s \geq z_i(t) \end{cases} \tag{3.1}$$

where τ is implicitly given by $\varphi_i(t;\tau,0) = s$ or, equivalently, $\varphi_i(\tau;t,s) = 0$.

Then integrating (3.1) with respect to s, and using changes of variable (here we have used Lemma 2.2), we obtain integral equations for $P_i(t)$, $i = 1, 2$,

$$
\begin{aligned}
P_i(t) &= \int_0^{z_i(t)} \frac{B_i(\tau)}{g_i(0, P_1(\tau), P_2(\tau))} e^{-\int_\tau^t \tilde{\mu}_i(\varphi_i(x;\tau,0), P_1(x), P_2(x))dx} ds \\
&\quad + \int_{z_i(t)}^m p_{i0}(\varphi_i(0;t,s)) e^{-\int_0^t \tilde{\mu}_i(\varphi_i(x;t,s), P_1(x), P_2(x))dx} ds \\
&= \int_0^t B_i(\tau) e^{-\int_\tau^t \mu_i(\varphi_i(x;\tau,0), P_1(x), P_2(x))dx} d\tau \\
&\quad + \int_0^m p_{i0}(\xi) e^{-\int_0^t \mu_i(\varphi_i(x;0,\xi), P_1(x), P_2(x))dx} d\xi.
\end{aligned}
\tag{3.2}
$$

In a similar way, we get integral equations for $B_i(t)$, $i = 1, 2$,

$$
\begin{aligned}
B_i(t) &= \int_0^t \beta_i(\varphi_i(t;\tau,0), P_1(t), P_2(t)) B_i(\tau) e^{-\int_\tau^t \mu_i(\varphi_i(x;\tau,0), P_1(x), P_2(x))dx} d\tau \\
&\quad + \int_0^m \beta_i(\varphi_i(t;0,\xi), P_1(t), P_2(t)) p_{i0}(\xi) e^{-\int_0^t \mu_i(\varphi_i(x;0,\xi), P_1(x), P_2(x))dx} d\xi.
\end{aligned}
\tag{3.3}
$$

Therefore, if $P_i(t)$ and $B_i(t)$ are nonnegative continuous solutions of (3.2) and (3.3), then $p_i(s,t)$ defined by (3.1) is a solution of system (2.1)-(2.3). Thus, proving the existence and uniqueness of solution of the basic system (2.1)-(2.3) is equivalent to showing that the integral equations (3.2) and (3.3) have a unique solution.

For $K > \max_{i=1,2}\{P_i(0)\}$, let $M_{T,K}$ be the closed subset of the Banach space $C([0,T])$ defined by

$$M_{T,K} = \{f \in C([0,T]) | 0 \leq f(t) \leq K\},$$

and $\|\cdot\|_T$ denotes the sup-norm on $M_{T,K}$. Then for each $(x,y) \in M_{T,K} \times M_{T,K}$, we define

$$\|(x,y)\|_T = \|x\|_T + \|y\|_T, \ M_{T,K}^2 = M_{T,K} \times M_{T,K}.$$

For each fixed $P := (P_1, P_2) \in M_{T,K}^2$, the equation (3.3) is a linear system of uncoupled Volterra integral equation for $B := (B_1, B_2)$, hence it has a unique nonnegative solution under the assumptions (A1)-(A4). Let such a solution be denoted by

$$B(t) = \mathcal{B}(P)(t), \ t \in [0, T],$$

or
$$B_1(t) = \mathcal{B}_1(P_1, P_2)(t), \ B_2(t) = \mathcal{B}_2(P_1, P_2)(t), \ t \in [0, T].$$
Substituting the solution (B_1, B_2) into (3.2), we see that (3.2) will be satisfied if and only if (P_1, P_2) is a fixed point of the operator
$$\mathcal{P}(P)(t) = \{\mathcal{P}_1(P_1, P_2)(t), \mathcal{P}_2(P_1, P_2)(t)\},$$
where $\mathcal{P}_1$ and $\mathcal{P}_2$ respectively denote the right sides of (3.2) for $i = 1, 2$.

Lemma 3.1 *Suppose that assumptions (A1)-(A4) hold. Then there exists a constant $T > 0$ for which (3.2) and (3.3) have a unique solution on $(0, T)$.*

Proof Since $M_{T,K}$ is closed, to complete the proof we only need to show that $\mathcal{P}$ maps $M_{T,K}^2$ into itself and that $\mathcal{P}$ is contractive for small T.

Step 1: $\mathcal{P}$ maps $M_{T,K}^2$ into itself.

From (3.3), it follows that
$$B_i(t) \le \beta_i^* P_{i0} + \beta_i^* \int_0^t B_i(\tau) d\tau, \ i = 1, 2.$$
By virtue of Gronwall's inequality, we obtain
$$B_i(t) \le \beta_i^* P_{i0} e^{\beta_i^* t}. \tag{3.4}$$
Combining the definition of $\mathcal{P}_i$ with (3.4), we have
$$\begin{aligned}
|\mathcal{P}_i(P)(t) - P_{i0}| &\le \int_0^t B_i(\tau) e^{-\int_\tau^t \mu_i(\varphi_i(x;\tau,0), P_1(x), P_2(x)) dx} d\tau \\
&\quad + \int_0^m p_{i0}(\xi) |1 - e^{-\int_0^t \mu_i(\varphi_i(x;0,\xi), P_1(x), P_2(x)) dx}| d\xi \\
&\le \int_0^t \beta_i^* P_{i0} e^{\beta_i^* \tau} d\tau + P_{i0} \le e^{\beta_i^* t} P_{i0}, \ i = 1, 2,
\end{aligned}$$
as a consequence of which we obtain
$$\|\mathcal{P}(P)(t) - P_0\|_T \le \sum_{j=1}^2 e^{\beta_j^* T} P_{j0} \le K \tag{3.5}$$
holds for T small enough, which is the conclusion.

Step 2: $\mathcal{P}$ is contractive.

For any $P^{(1)} := (P_1^{(1)}, P_2^{(1)})$ and $P^{(2)} := (P_1^{(2)}, P_2^{(2)})$ belong to $M_{T,K}^2$, letting $B^{(1)}$ and $B^{(2)}$ be the solutions of (3.3) corresponding to $P^{(1)}$ and $P^{(2)}$, respectively. In order to simplify the expressions, we denote
$$\bar{\mu}_i^{(j)} := \mu_i(\varphi_i^{(j)}(t;\tau,0), P^{(j)}(t)), \quad \mu_i^{(j)} := \mu_i(\varphi_i^{(j)}(t;0,\xi), P^{(j)}(t)) \text{ and}$$
$$\bar{\beta}_i^{(j)} := \beta_i(\varphi_i^{(j)}(t;\tau,0), P^{(j)}(t)), \quad \beta_i^{(j)} := \beta_i(\varphi_i^{(j)}(t;0,\xi), P^{(j)}(t)) \ (i, j = 1, 2).$$
Then from (3.2), we have
$$\begin{aligned}
\left| \mathcal{P}_1(P^{(1)})(t) - \mathcal{P}_1(P^{(2)})(t) \right| &= \Big| \int_0^t [\mathcal{B}_1(P^{(1)}(\tau)) - \mathcal{B}_1(P^{(2)}(\tau))] e^{-\int_\tau^t \bar{\mu}_1^{(1)} dx} d\tau \\
&\quad + \int_0^t \mathcal{B}_1(P^{(2)}(\tau)) [e^{-\int_\tau^t \bar{\mu}_1^{(1)} dx} - e^{-\int_\tau^t \bar{\mu}_1^{(2)} dx}] d\tau \\
&\quad + \int_0^m p_{10}(\xi) [e^{-\int_\tau^t \mu_1^{(1)} dx} - e^{-\int_\tau^t \mu_1^{(2)} dx}] d\xi \Big| \\
&\le \int_0^t |\mathcal{B}_1(P^{(1)}(\tau)) - \mathcal{B}_1(P^{(2)}(\tau))| d\tau
\end{aligned} \tag{1}$$

$$+ \int_0^t \mathcal{B}_1(P^{(2)}(\tau)) \int_\tau^t |\bar{\mu}_1^{(1)} - \bar{\mu}_1^{(2)}| dx d\tau$$

$$+ \int_0^m p_{10}(\xi) \int_0^t |\mu_1^{(1)} - \mu_1^{(2)}| dx d\xi, \tag{3.6}$$

where we used that $|e^x - e^y| \leq |x - y|, \ \forall x, y \leq 0$.

We now estimate the integrals in (3.6). Let $|\mathcal{F}_1(t)| = |\mathcal{B}_1(P^{(1)}(t)) - \mathcal{B}_1(P^{(2)}(t))|$. From (3.3) and (3.4), it follows that

$$|\mathcal{F}_1(t)| \leq \beta_1^* \int_0^t |\mathcal{F}_1(\tau)| d\tau + J_1(t). \tag{3.7}$$

Here

$$J_1(t) = \beta_1^* P_{10} e^{\beta_1^* t} \int_0^t |\bar{\beta}_1^{(1)} e^{-\int_\tau^t \bar{\mu}_1^{(1)} dx} - \bar{\beta}_1^{(2)} e^{-\int_\tau^t \bar{\mu}_1^{(2)} dx}| d\tau$$
$$+ \int_0^m |\beta_1^{(1)} e^{-\int_0^t \mu_1^{(1)} dx} - \beta_1^{(2)} e^{-\int_0^t \mu_1^{(2)} dx}| p_{10}(\xi) d\xi.$$
$$\leq \beta_1^* P_{10} e^{\beta_1^* t} \int_0^t |\bar{\beta}_1^{(1)} - \bar{\beta}_1^{(2)}| d\tau + \beta_1^* P_{10} e^{\beta_1^* t} \beta_1^* \int_0^t \int_\tau^t |\bar{\mu}_1^{(1)} - \bar{\mu}_1^{(2)}| dx d\tau$$
$$+ \int_0^m |\beta_1^{(1)} - \beta_1^{(2)}| p_{10}(\xi) d\xi + \int_0^\infty \int_0^t |\mu_1^{(1)} - \mu_1^{(2)}| dx p_{10}(\xi) d\xi$$
$$\leq \left(1 + L_{g_1} t e^{L_{g_1} t}\right) \left(L_{\beta_1} + \beta_1^* L_{\mu_1} t\right) \left(\beta_1^* e^{\beta_1^* t} + 1\right) P_{10} \|P^{(1)} - P^{(2)}\|_T$$
$$:= \zeta_1(t) \|P^{(1)} - P^{(2)}\|_T,$$

where we have used the fact that, for $t \geq t_0$,

$$|\varphi_1^{(1)}(t; t_0, s_0) - \varphi_1^{(2)}(t; t_0, s_0)| \leq L_{g_1} \int_{t_0}^t e^{L_{g_1}(t-x)} |P^{(1)}(x) - P^{(2)}(x)| dx,$$

which follows from (2.5) and Gronwall's inequality, and we also have used the derivation of the bound of $\int_0^t |\bar{\beta}_1^{(1)} - \bar{\beta}_1^{(2)}| d\tau$ (in a similar way for the rest terms)

$$\int_0^t |\bar{\beta}_1^{(1)} - \bar{\beta}_1^{(2)}| d\tau \leq \int_0^t L_{\beta_1} \left(|\varphi_1^{(1)}(t; \tau, 0) - \varphi_1^{(2)}(t; \tau, 0)| + |P^{(1)}(t) - P^{(2)}(t)|\right) d\tau$$
$$\leq \int_0^t L_{\beta_1} \left(L_{g_1} \int_\tau^t e^{L_{g_1}(t-x)} |P^{(1)}(x) - P^{(2)}(x)| dx + |P^{(1)}(t) - P^{(2)}(t)|\right) d\tau$$
$$\leq L_{\beta_1} \left(t L_{g_1} e^{L_{g_1} t} \int_0^t |P^{(1)}(x) - P^{(2)}(x)| dx + t |P^{(1)}(t) - P^{(2)}(t)|\right)$$
$$\leq t L_{\beta_1} \left(1 + t L_{g_1} e^{L_{g_1} t}\right) \|P^{(1)} - P^{(2)}\|_T .$$

Hence, from (3.7) we obtain

$$|\mathcal{F}_1(t)| \leq \beta_1^* \int_0^t |\mathcal{F}_1(\tau)| d\tau + \zeta_1(T) \|P^{(1)} - P^{(2)}\|_T$$

and, by virtue of Gronwall's inequality, it follows that for $\forall t \in [0, T]$,

$$|\mathcal{F}_1(t)| \leq \zeta_1(T) e^{\beta_1^* T} \|P^{(1)} - P^{(2)}\|_T.$$

Using this estimate in the first term of (3.6), we obtain that

$$\int_0^t |\mathcal{B}_1(P^{(1)}(\tau)) - \mathcal{B}_1(P^{(2)}(\tau))| d\tau \leq T \zeta_1(T) e^{\beta_1^* T} \|P^{(1)} - P^{(2)}\|_T. \tag{3.8}$$

In a similar way, we derive that

$$\int_0^t \mathcal{B}_1(P^{(2)}(\tau)) \int_\tau^t |\bar{\mu}_1^{(1)} - \bar{\mu}_1^{(2)}| dx d\tau \leq T \left(1 + L_{g_1} T e^{L_{g_1} T}\right) \beta_1^* e^{\beta_1^* T} L_{\mu_1} P_{10} T \|P^{(1)} - P^{(2)}\|_T, \tag{3.9}$$

and

$$\int_0^m p_{10}(\xi) \int_0^t |\mu_1^{(1)} - \mu_1^{(2)}| dx d\xi \leq T L_{\mu_1} \left(1 + L_{g_1} T e^{L_{g_1} T}\right) P_{10} \|P^{(1)} - P^{(2)}\|_T. \tag{3.10}$$

Putting (3.8)-(3.10) together, one may write

$$\left|\mathcal{P}_1(P^{(1)})(t) - \mathcal{P}_1(P^{(2)})(t)\right| \leq M_1 \|P^{(1)} - P^{(2)}\|_T,$$

which, with a similar bound for $\left|\mathcal{P}_2(P^{(1)})(t) - \mathcal{P}_2(P^{(2)})(t)\right|$, leads to

$$\left|\mathcal{P}(P^{(1)})(t) - \mathcal{P}(P^{(2)})(t)\right| \le M\|P^{(1)} - P^{(2)}\|_T,$$

where $M = M(\beta_i^*, L_{\mu_i}, L_{g_i}, L_{\beta_i}, \|p_{i0}\|_{L^1}, T)$ is a continuous increasing function of T vanishing for $T = 0$. For T sufficiently small, we claim that the map $\mathcal{P}$ is contractive. Hence (3.2) and (3.3) have a unique solution for $0 \le t \le T$ when T small enough. $\square$

In order to establish the global existence result for (3.2) and (3.3), we set the following hypothesis related to the boundedness of the birth and death rates, μ_i and β_i, $i = 1, 2$

$$(A5) \qquad M_2 := \max_{i=1,2} \left\{ \sup_{(s,P_1,P_2)\in[0,m]\times(0,\infty)\times(0,\infty)} \{\beta_i(s, P_1, P_2) - \mu_i(s, P_1, P_2)\} \right\} < \infty$$

Lemma 3.2 *Let $p_i(s,t)$ be a solution of (3.2) and (3.3) up to time T and assume that (A5) is satisfied, then $P_i(t)$ is a continuously differentiable function in $(0,T)$ and satisfies the following bound*

$$P_i(t) \le P_i(0)e^{M_2 t}, \forall t \in [0, T].$$

Proof It follows from the fact that $P_i(t)$ satisfies the integro-differential equation

$$P_i'(t) = \int_0^m (\beta_i(s, P_1(t), P_2(t)) - \mu_i(s, P_1(t), P_2(t)))p_i(s,t)\mathrm{d}s$$

which is easily obtained by differentiating the expression (3.2) with respect to t, so that $P_i(t)$ also satisfies the differential inequality $P_i'(t) \le M_2 P_i(t)$, which implies the statement of the lemma. $\square$

Theorem 3.3 *Suppose that assumptions (A1)-(A5) hold. Then system (2.1)-(2.3) has a unique solution for all positive time.*

The proof is essentially the same as that of Theorem 3 in [5], and hence is omitted.

In what follows, we analyze the existence of equilibrium solution of system (2.1)-(2.3). Clearly, any equilibrium solution $(p_1^*(s), p_2^*(s))$ satisfies the following $(i = 1, 2)$:

$$\frac{d(g_i(s, P_1^*, P_2^*)p_i^*(s))}{ds} = -\mu_i(s, P_1^*, P_2^*)p_i^*(s) , \tag{3.11}$$

$$p_i^*(0) = \int_0^m \gamma_i(s, P_1^*, P_2^*)p_i^*(s)\mathrm{d}s , \tag{3.12}$$

$$P_i^* = \int_0^m p_i^*(s)ds , \tag{3.13}$$

where $\gamma_i(s, P_1(t), P_2(t)) = \dfrac{\beta_i(s, P_1(t), P_2(t))}{g_i(0, P_1(t), P_2(t))}$. The general solution of Eq. (3.11) is found as

$$p_i^*(s) = p_i^*(0)\Pi_i(s, P_1^*, P_2^*), \tag{3.14}$$

where

$$\Pi_i(s, P_1, P_2) \stackrel{def}{=} \exp\left\{-\int_0^s \frac{\partial x g_i(x, P_1, P_2) + \mu_i(x, P_1, P_2)}{g_i(x, P_1, P_2)}\mathrm{d}x\right\}. \tag{3.15}$$

By integration of Eq.(3.14) we obtain

$$p_i^*(0) = \frac{P_i^*}{\int_0^m \Pi_i(s, P_1^*, P_2^*)\mathrm{d}s}, \tag{3.16}$$

substituting Eq.(3.16) into Eq.(3.14) we see that

$$p_i^*(s) = \frac{P_i^*\Pi_i(s, P_1^*, P_2^*)}{\int_0^m \Pi_i(s, P_1^*, P_2^*)\mathrm{d}s}. \tag{3.17}$$

Substituting Eqs.(3.14) and (3.16) into Eq.(3.12) we obtain

$$1 = \int_0^m \gamma_i(s, P_1^*, P_2^*) \Pi_i(s, P_1^*, P_2^*) \mathrm{d}s =: R_i(P_1^*, P_2^*). \tag{3.18}$$

Thus, we have shown that a necessary and sufficient condition for the existence of a nonnegative solution $(p_1^*(s), p_2^*(s))$ of system (3.11)-(3.13) is that there exists a pair of positive constants (P_1^*, P_2^*) satisfying the Eq. (3.18), and the solution is determined by Eq. (3.17).

Theorem 3.4 *Suppose the following hold:*

$$R_i(0, 0) > 1, \quad \frac{\partial R_i}{\partial P_j} < 0, \ i, j = 1, 2, \tag{3.19}$$

$$(P_1^{(1)} - P_1^{(2)})(P_2^{(1)} - P_2^{(2)}) < 0, \tag{3.20}$$

where $P_1^{(i)}$ and $P_2^{(i)}$ denote the unique solution of equations $R_i(P_1, 0) = 1$ and $R_i(0, P_2) = 1$, respectively. Then there exists a pair of positive constants (P_1^*, P_2^*) satisfying the Eq. (3,18).

Proof By condition (3.19), we can easily derive the existence and uniqueness of solutions to the equations $R_i(P_1, 0) = 1$ and $R_i(0, P_2) = 1$.

Consequently, we consider two elements of the surfaces defined by

$$z = R_1(P_1, P_2), \text{and} \quad z = R_2(P_1, P_2), \ P_1 \geq 0, \ P_2 \geq 0.$$

Hence by (3.19) the intersection of these two surfaces with the plane $z = 1$ define two curves on the plane. These two curves are defined by

$$R_1(P_1, P_2) = 1, \ R_2(P_1, P_2) = 1, \ P_1 \geq 0, \ P_2 \geq 0,$$

which by (3.20) will intersect at a point, say (P_1^*, P_2^*) with $P_1^* > 0, P_2^* > 0$.   □

§4   The linearized system and its regularity properties

Given a stationary distribution $p_i^*(s)$ of system (2.1)-(2.3). To examine the stability of the size distributions $p_1^*(s)$ and $p_2^*(s)$, we denote by $u_i(s, t)$ the perturbation of $p_i^*(s)$. Dropping all of the nonlinear terms, we arrive at the following linearized system ($i = 1, 2, \ t > 0$)

$$\frac{\partial u_i(s, t)}{\partial t} + g_i(s, P_1^*, P_2^*) \frac{\partial u_i(s, t)}{\partial s} + \left(\frac{\partial g_i}{\partial s} + \mu_i\right) u_i(s, t) + \sum_{j=1}^2 \Delta_{ij}(s) U_j(t) = 0, \tag{4.1}$$

$$u_i(0, t) = \int_0^m \gamma_i(s, P_1^*, P_2^*) u_i(s, t) \mathrm{d}s + \int_0^m p_i^*(s) \left[\sum_{j=1}^2 \frac{\partial \gamma_i}{\partial P_j} U_j(t)\right] ds, \tag{4.2}$$

where

$$U_j(t) = \int_0^m u_j(s, t) \mathrm{d}s, \tag{4.3}$$

$$\Delta_{ij}(s) = \frac{\partial^2 g_i}{\partial s \partial P_j} p_i^*(s) + \frac{\partial \mu_i}{\partial P_j} p_i^*(s) + \frac{\partial g_i}{\partial P_j} \frac{\partial p_i^*}{\partial s}, \ j = 1, 2. \tag{4.4}$$

Let $\mathcal{X}$ be the product space $L^1(0, m) \times L^1(0, m)$. Define the bounded linear functional Φ_i on $\mathcal{X}$ by

$$\Phi_i(u_1, u_2)^T = \int_0^m \gamma_i(s, P_1^*, P_2^*) u_i(s, t) \mathrm{d}s + \int_0^m p_i^*(s) \left[\sum_{j=1}^2 \frac{\partial \gamma_i}{\partial P_j} U_j(t)\right] ds, \tag{4.5}$$

and the operators

$$\mathcal{A} \begin{pmatrix} u_1 \\ u_2 \end{pmatrix} = - \begin{pmatrix} g_1(\cdot, P_1^*, P_2^*)\frac{\partial u_1}{\partial s} \\ g_2(\cdot, P_1^*, P_2^*)\frac{\partial u_2}{\partial s} \end{pmatrix},$$

with $Dom(\mathcal{A}) = \{(u_1, u_2)^T \in W^{1,1}(0, m) \times W^{1,1}(0, m)|\, u_i(0) = \Phi_i(u_1, u_2)^T\}$,

$$\mathcal{B} \begin{pmatrix} u_1 \\ u_2 \end{pmatrix} = - \begin{pmatrix} (\frac{\partial g_1(\cdot, P_1^*, P_2^*)}{\partial s} + \mu_1(\cdot, P_1^*, P_2^*))u_1 \\ \frac{\partial g_2(\cdot, P_1^*, P_2^*)}{\partial s} + \mu_2(\cdot, P_1^*, P_2^*))u_2 \end{pmatrix} \quad \text{on } \mathcal{X},$$

$$\mathcal{C} \begin{pmatrix} u_1 \\ u_2 \end{pmatrix} = \begin{pmatrix} \sum_{j=1}^2 \Delta_{1j}(s)U_j(t) \\ \sum_{j=1}^2 \Delta_{2j}(s)U_j(t) \end{pmatrix} \quad \text{on } \mathcal{X}.$$

Then the linearized system (4.1)-(4.4) can be cast in the form of an abstract ordinary differential equation on $\mathcal{X}$

$$\frac{d}{dt}(u_1, u_2)^T = (\mathcal{A} + \mathcal{B} + \mathcal{C})(u_1, u_2)^T,$$

with the initial data

$$(u_1(0), u_2(0))^T = (u_{01}, u_{02})^T,$$

where ^{T} denotes the transpose.

Theorem 4.1. *The operator $\mathcal{A} + \mathcal{B} + \mathcal{C}$ generates a strongly continuous semigroup $\{\mathcal{T}(t)\}_{t \geq 0}$ of bounded linear operators on $\mathcal{X}$.*

Proof. Since the operator $\mathcal{B} + \mathcal{C}$ is bounded on $\mathcal{X}$, it suffices to prove that $\mathcal{A}$ generates a strongly continuous semigroup. To this end, we introduce the modified operator

$$\mathcal{A}_0(u, T_1, T_2)^T = (-g_1(\cdot, P_1^*, P_2^*)\frac{\partial u_1}{\partial s}, g_2(\cdot, P_1^*, P_2^*)\frac{\partial u_2}{\partial s}),$$

with $Dom(\mathcal{A}_0) = \{(u_1, u_2)^T \in W^{1,1}(0, m) \times W^{1,1}(0, m))|\, u_i(0) = 0\}$.

Since g_i is positive, it is obvious that $\mathcal{A}_0$ is invertible and generates a strongly continuous semigroup $\{\mathcal{T}_0(t)\}_{t \geq 0}$ on $\mathcal{X}$, given by

$$(\mathcal{T}_0(t)(u_1, u_2)^T)(s) = \begin{cases} (u_1(\Gamma_1^{-1}(\Gamma_1(s, P_1^*, P_2^*) - t)), u_2(\Gamma_2^{-1}(\Gamma_2(s, P_1^*, P_2^*) - t)))^T, \\ \qquad\qquad\qquad\qquad\qquad \text{if } \Gamma_i(s, P_1^*, P_2^*) \geq t, \\ (0, 0)^T, \qquad \text{otherwise,} \end{cases}$$

where

$$\Gamma_i(s, P_1, P_2) = \int_0^s \frac{1}{g_i(y, P_1, P_2)} \mathrm{d}y.$$

For simplicity, we assume $\Gamma_1(s, P_1^*, P_2^*) = \Gamma_2(s, P_1^*, P_2^*), s \in [0, m]$.

Let $\mathcal{X}_{-1}$ be the completion of $\mathcal{X}$ in the norm $\| \cdot \|_{-1} \overset{def}{=} \|\mathcal{A}_0^{-1} \cdot \|$, define the extended semigroup $\{\mathcal{T}_{-1}(t)\}_{t \geq 0}$ on $\mathcal{X}_{-1}$ by

$$\mathcal{T}_{-1}(t) = \mathcal{A}_0 \mathcal{T}_0(t) \mathcal{A}_0^{-1},$$

and denote its generator by $\mathcal{A}_{-1}$. Then $\mathcal{A}_{-1}$ is an extension of $\mathcal{A}_0$ with $Dom(\mathcal{A}_{-1}) = \mathcal{X}$ and range in $\mathcal{X}_{-1}$. Finally we define the perturbing operator $\mathcal{P} \in L(\mathcal{X}, \mathcal{X}_{-1})$ by

$$\mathcal{P} \begin{pmatrix} u_1 \\ u_2 \end{pmatrix} \overset{def}{=} \begin{pmatrix} -\Phi_1(u_1, u_2)^T & 0 \\ -\Phi_2(u_1, u_2)^T & 0 \end{pmatrix} \mathcal{A}_{-1} \begin{pmatrix} 1 \\ 0 \end{pmatrix}$$

where $1 = 1(\cdot)$ is the constant function 1 in $L^1(0, m)$. Then the operator $\mathcal{A}$ is just the part of the operator $\mathcal{A}_{-1} + \mathcal{P}$ in $\mathcal{X}$. If we could prove that operator $\mathcal{A}_{-1} + \mathcal{P}|_{\mathcal{X}}$ generates a strongly continuous semigroup on $\mathcal{X}$, then the theorem is also proved. To do so , we apply the Desch-

Schappacher Perturbation Theorem (see [26] and also [13,14]). For given $(h_1, h_2)^T \in \mathcal{X}$, we need to show that the following relation is true:

$$\int_0^m \mathcal{T}_{-1}(m-t)\mathcal{P}\left(h_1(t), h_2(t)\right)^T \mathrm{d}t =$$

$$\mathcal{A}_{-1} \int_0^m \begin{pmatrix} -\Phi_1(h_1(t), h_2(t))^T & 0 \\ -\Phi_2(h_1(t), h_2(t))^T & 0 \end{pmatrix} \mathcal{T}_{-1}(m-t) \begin{pmatrix} 1(\cdot) \\ 0 \end{pmatrix} \mathrm{d}t \quad \text{on } \mathcal{X}.$$

Since the above relation is equivalent to

$$\int_0^m \begin{pmatrix} -\Phi_1(h_1(t), h_2(t))^T & 0 \\ -\Phi_2(h_1(t), h_2(t))^T & 0 \end{pmatrix} \mathcal{T}_0(m-t) \begin{pmatrix} 1(\cdot) \\ 0 \end{pmatrix} \mathrm{d}t \in Dom(\mathcal{A}_0),$$

and

$$\int_0^m \begin{pmatrix} -\Phi_1(h_1(t), h_2(t))^T & 0 \\ -\Phi_2(h_1(t), h_2(t))^T & 0 \end{pmatrix} \mathcal{T}_0(m-t) \begin{pmatrix} 1(\cdot) \\ 0 \end{pmatrix} \mathrm{d}t =$$

$$\int_{m-\Gamma_i(\cdot, P_1^*, P_2^*)}^m \begin{pmatrix} -\Phi_1(h_1(t), h_2(t))^T \\ -\Phi_2(h_1(t), h_2(t))^T \end{pmatrix} \mathrm{d}t,$$

the proof is complete. $\square$

By means of Riesz-Schauder Theory, we have the following

Theorem 4.2. *The spectrum of the semigroup generator $\mathcal{A} + \mathcal{B} + \mathcal{C}$ consists of isolated eigenvalues of finite multiplicity.*

Because of Theorem 4.2, the linear stability of the stationary solution is spectrally determined (see [26]). Our analysis would be much simpler if the eigenvalue with largest real part were real. The following result enables us to draw this conclusion in certain circumstances.

Theorem 4.3. *Suppose that*

$$\Delta_{ij} \leq 0, \frac{\partial \gamma_i}{\partial P_j} \geq 0, \qquad i, j = 1, 2, \tag{4.6}$$

where Δ_{ij} is given by (4.4). Then the semigroup $\{\mathcal{T}(t)\}_{t \geq 0}$ generated by the operator $\mathcal{A} + \mathcal{B} + \mathcal{C}$ is positive.

Proof. The condition (4.6) ensures that the operator $\mathcal{C}$ is positive. Hence it suffices to prove that the operator $\mathcal{A} + \mathcal{B}$ is nonnegative. Suppose that u_i is a solution of the following equation

$$\frac{d}{dt} \begin{pmatrix} u_1 \\ u_2 \end{pmatrix} = (\mathcal{A} + \mathcal{B}) \begin{pmatrix} u_1 \\ u_2 \end{pmatrix}, \quad \begin{pmatrix} u_1(0) \\ u_2(0) \end{pmatrix} = \begin{pmatrix} u_{01} \\ u_{02} \end{pmatrix} \in Dom(\mathcal{A}).$$

Then the function v_i defined by

$$v_i(s, t) = u_i(s, t) \exp\{\int_0^s \Theta_i(y, P_1^*, P_2^*) \mathrm{d}y\},$$

with

$$\Theta_i(s, R_1, R_2) = \frac{g_{is}(s, P_1, P_2) + \mu_i(s, P_1, P_2)}{g_i(s, P_1, P_2)}$$

satisfies

$$v_{it}(s, t) + g_i(s, P_1^*, P_2^*)v_{is}(s, t) = 0,$$

$$v_i(0, t) = \Phi_i \begin{pmatrix} v_1(\cdot, t)exp\{-\int_0^s \Theta_1(y, P_1^*, P_2^*)\mathrm{d}y\} \\ v_2(\cdot, t)exp\{-\int_0^s \Theta_2(y, P_1^*, P_2^*)\mathrm{d}y\} \end{pmatrix} \overset{def}{=} \Phi_i^* \begin{pmatrix} v_1(\cdot, t) \\ v_2(\cdot, t) \end{pmatrix},$$

$$v_i(s, 0) = v_{i0}(s),$$

which corresponds to the following modified semigroup generator

$$\mathcal{A}_m(v_1, v_2)^T = -(g_1(\cdot, P_1^*, P_2^*)v_{1s}, g_2(\cdot, P_1^*, P_2^*)v_{1s})^T, \tag{4.7}$$

with $Dom(\mathcal{A}_m) = \left\{ \begin{pmatrix} v_1 \\ v_2 \end{pmatrix} \in W^{1,1}(0,m) \times W^{1,1}(0,m) \mid v_i(0) = \Phi_i^* \begin{pmatrix} v_1 \\ v_2 \end{pmatrix} \right\}.$

For $\lambda \geq 0$ sufficiently large and $h_1, h_2 \in L^1(0,m)$, the resolvent equation is

$$\lambda(v_1, v_2)^T - \mathcal{A}_m(v_1, v_2)^T = (h_1, h_2)^T. \tag{4.8}$$

Substituting Eq.(4.7) into Eq.(4.8) and applying Φ_i^*, we are able to obtain

$$\Phi_i^* \begin{pmatrix} v_1 \\ v_2 \end{pmatrix} = \left(1 - \Phi_i^* \begin{pmatrix} e^{-\lambda \Gamma_1(\cdot, P_1^*, P_2^*)} \\ e^{-\lambda \Gamma_2(\cdot, P_1^*, P_2^*)} \end{pmatrix} \right)^{-1} \Phi_i^* \left(\begin{pmatrix} \int_0^\cdot e^{\lambda(\Gamma_1(x, P_1^*, P_2^*) - \Gamma_1(\cdot, P_1^*, P_2^*))} \frac{h_1(x)}{g_1(x, P_1^*, P_2^*)} dx \\ \int_0^\cdot e^{\lambda(\Gamma_2(x, P_1^*, P_2^*) - \Gamma_2(\cdot, P_1^*, P_2^*))} \frac{h_2(x)}{g_2(x, P_1^*, P_2^*)} dx \end{pmatrix} \right).$$

From condition (4.6), it can be seen that Φ_i^* is positive operator, hence for such λ the resolvent operator of $\mathcal{A}_m$ (or equivalently of $\mathcal{A} + \mathcal{B}$) is positive. The proof is complete. $\square$

The following corollary can be proved by means of the theory of positive semigroups (see [26] and also [13,14] for relative results).

Corollary 4.4. *Suppose that the condition (4.6) is satisfied, then $s(\mathcal{A} + \mathcal{B} + \mathcal{C}) \in \sigma(\mathcal{A} + \mathcal{B} + \mathcal{C})$ and $s(\mathcal{A} + \mathcal{B} + \mathcal{C})$ is a dominant eigenvalue, where $s(\mathcal{A} + \mathcal{B} + \mathcal{C})$ denotes the bound of the spectrum of the operator $\mathcal{A} + \mathcal{B} + \mathcal{C}$.*

§5   The characteristic equation and stability results

In the light of the positivity conditions deduced in the previous section, the linear stability of stationary solutions of system (4.1)-(4.4) is determined by the eigenvalues of the semigroup generator $\mathcal{A} + \mathcal{B} + \mathcal{C}$. In this section we derive a characteristic equation to discuss the eigenvalues.

Consider the solutions to the system (4.1)-(4.4) in the following form

$$(u_1(s,t), u_2(s,t))^T = (e^{\lambda t} \bar{u}_1(s), e^{\lambda t} \bar{u}_2(s)). \tag{5.1}$$

Substituting (5.1) into Eqs.(4.1)-(4.2) and dividing by $e^{\lambda t}$, we have

$$(\lambda + \mu_i + \frac{\partial g_i}{\partial s}) \bar{u}_i(s) + g_i(s, P_1^*, P_2^*) \frac{\partial \bar{u}_i(s)}{\partial s} + \sum_{j=1}^2 \Delta_{ij}(s) \bar{U}_j = 0, \tag{5.2}$$

$$\bar{u}_i(0) = \int_0^m \gamma_i(s, P_1^*, P_2^*) \bar{u}_i(s) ds + \int_0^m p_i^*(s) \left[\sum_{j=1}^2 \frac{\partial \gamma_i}{\partial P_j} \bar{U}_j \right] ds, \tag{5.3}$$

where

$$\bar{U}_j = \int_0^m \bar{u}_j(s) ds.$$

Integrating (5.2) on $[0, m]$, using the fact that $g_i(m, \cdot, \cdot) = 0$ and Eq. (5.3), we obtain that

$$(\lambda - A_{11}) \bar{U}_1 - A_{12} \bar{U}_2 = \int_0^m (\beta_1(s, P_1^*, P_2^*) - \mu_1(s, P_1^*, P_2^*)) \bar{u}_1(s) ds, \tag{5.4}$$

$$-A_{21} \bar{U}_1 + (\lambda - A_{22}) \bar{U}_2 = \int_0^m (\beta_2(s, P_1^*, P_2^*) - \mu_2(s, P_1^*, P_2^*)) \bar{u}_2(s) ds, \tag{5.5}$$

where

$$A_{ij} = \int_0^m \left(\Delta_{ij}(s) + g_i(0, P_1^*, P_2^*) p_i^*(s) \frac{\partial \gamma_i}{\partial P_j} \right) ds, \qquad i,j = 1,2. \tag{5.6}$$

The solution of Eq. (5.2) is given by

$$\bar{u}_i(s) = \left(\bar{u}_i(0) - \int_0^s \frac{\sum_{j=1}^2 \Delta_{ij}(s)\bar{U}_j}{g_i \Psi_i} dy \right) \Psi_i(\lambda, s, P_1^*, P_2^*), \tag{5.7}$$

where

$$\Psi_i(\lambda, s, P_1, P_2) = e^{-\int_0^s \frac{(\lambda + \mu_i + \partial_s g_i)}{g_i} dy}.$$

From the Eq. (5.3), it follows that

$$\bar{u}_i(s) = \frac{\Psi_i}{1 - \int_0^m \gamma_i \Psi_i ds} \int_0^m \left\{ p_i^*(s) \left[\sum_{j=1}^2 \frac{\partial \gamma_i}{\partial P_j} \bar{U}_j \right] \right.$$
$$\left. - \gamma_i \Psi_i \int_0^s \frac{\sum_{j=1}^2 \Delta_{ij}(s)\bar{U}_j}{g_i \Psi_i} dy \right\} ds - \int_0^s \frac{\sum_{j=1}^2 \Delta_{ij}(s)\bar{U}_j}{g_i \Psi_i} dy \Psi_i. \tag{5.8}$$

Now supplying (5.8) in (5.4) and (5.5), respectively, and introducing the notations

$$G_{ij}(\lambda) = (1 - \int_0^m \gamma_i \Psi_i ds)^{-1} \int_0^m (\beta_i - \mu_i) \Psi_i ds$$
$$\times \int_0^m \left[p_i^*(s) \frac{\partial \gamma_i}{\partial P_j} - \gamma_i \Psi_i \int_0^s \frac{\Delta_{ij}(s)}{g_i \Psi_i} dy \right] ds$$
$$- \int_0^m (\beta_i - \mu_i) \Psi_i \int_0^s \frac{\Delta_{ij}(s)}{g_i \Psi_i} dy ds, \qquad i,j = 1,2, \tag{5.9}$$

we obtain the following conditions for the constants λ, $\bar{U}_1$ and $\bar{U}_2$:

$$(\lambda - A_{11} - G_{11}(\lambda))\bar{U}_1 - (A_{12} + G_{12}(\lambda))\bar{U}_2 = 0 , \tag{5.10}$$

$$-(A_{21} + G_{21}(\lambda))\bar{U}_1 + (\lambda - A_{22} - G_{22}(\lambda))\bar{U}_2 = 0 , \tag{5.11}$$

which has nonzero solutions $(\bar{U}_1, \bar{U}_2)$ if and only if its determinant of coefficients vanishes. Therefore we have shown the following

Theorem 5.1. *The spectrum of the semigroup generator $\mathcal{A} + \mathcal{B} + \mathcal{C}$ consists of all of the roots of the characteristic equation $f(\lambda) = 0$, where the function f is given by*

$$f(\lambda) \stackrel{def}{=} \begin{vmatrix} \lambda - A_{11} - G_{11}(\lambda) & -(A_{12} + G_{12}(\lambda)) \\ -(A_{21} + G_{21}(\lambda)) & \lambda - A_{22} - G_{22}(\lambda) \end{vmatrix}. \tag{5.12}$$

Theorem 5.2. *Given a positive stationary solution (P_1^*, P_2^*), if the condition (4.6) holds, then the stationary solution is linearly unstable when $f(0) < 0$.*

Proof. Due to the condition (4.6), we invoke Corollary 4.4 and restrict ourselves to $\lambda \in \mathbb{R}$. It is easy to show that $\lim_{\lambda \to +\infty} \Psi_i(\lambda, s, P_1^*, P_2^*) = 0, i = 1, 2$. Since for $0 \leq y < s \leq m$, $\Gamma_i(y, P_1^*, P_2^*) < \Gamma_i(s, P_1^*, P_2^*)$, thus

$$\lim_{\lambda \to +\infty} \exp\{\lambda(\Gamma_i(y, P_1^*, P_2^*) - \Gamma_i(s, P_1^*, P_2^*))\} = 0.$$

Then, by the definition of Ψ_i, it is clear that

$$\lim_{\lambda \to +\infty} \int_0^m \Psi_i(\lambda, s, P_1^*, P_2^*) \int_0^s \frac{1}{\Psi_i(\lambda, y, P_1^*, P_2^*)} dy ds = 0.$$

Hence it follows from (5.9) that $\lim\limits_{\lambda \to +\infty} G_{ij}(\lambda) = 0, i, j = 1, 2$, which imply that

$$\lim_{\lambda \to +\infty} f(\lambda) = +\infty.$$

On the other hand, $f(\lambda)$ is continuous in λ. Hence $f(\lambda) = 0$ has a positive root if $f(0) < 0$, i.e., the semigroup generator has a positive eigenvalue. The proof is complete. $\square$

Theorem 5.3. *For a positive stationary solution* (P_1^*, P_2^*), *suppose that the condition (4.6) and the following hold,*

$$A_{12} \geq 0, \ A_{21} \geq 0, \tag{5.13}$$

$$A_{11} + G_{11}(0) \leq 0, \ A_{22} + G_{22}(0) \leq 0. \tag{5.14}$$

Then the stationary distribution $p_i^*(s)$ *is linearly asymptotically stable if* $f(0) > 0$.

Proof. Because of the condition (4.6), Corollary 4.4 works. Let λ be real. Then the spectrum of the semigroup generator is either empty or contains a dominant real eigenvalue. If the dominant eigenvalue is negative, then the growth bound of the semigroup are contained in $[-\infty, 0)$. By the proof of Theorem 5.2 we have $\lim\limits_{\lambda \to +\infty} f(\lambda) = +\infty$. When $f(0) > 0$, the stationary solution will be linearly asymptotically stable if we can show that $f(\lambda)$ is nondecreasing for $\lambda \geq 0$ due to theorem 5.1. In what follows we show that $f'(\lambda) \geq 0, \lambda \geq 0$.

Clearly,

$$f'(\lambda) = (1 - G'_{11}(\lambda))(\lambda - A_{22} - G_{22}(\lambda)) - G'_{21}(\lambda)(A_{12} + G_{12}(\lambda))$$
$$+ (1 - G'_{22}(\lambda))(\lambda - A_{11} - G_{11}(\lambda)) - G'_{12}(\lambda)(A_{21} + G_{21}(\lambda)). \tag{5.15}$$

Making the use of the conditions (4.6) and the assumptions (A1)-(A4), we get the following relations:

$$G'_{ij}(\lambda) \leq 0, G_{ij}(\lambda) \geq 0, \ i, j = 1, 2. \tag{5.16}$$

Putting (5.13)-(5.16) together, one may see that all terms in $f'(\lambda)$ are nonnegative. The proof is complete. $\square$

§6   Concluding remarks

Our conclusion in this paper is a generalization of age-structured population models. Note that the particular case $g_i(s, P_1, P_2) \equiv 1, \ i = 1, 2$ is nothing but an age-structured one. Moreover, some results of the age-independent Kolmogorov system and the age-dependent Lotka-Volterra-type two-species competition system can be recovered from our results.

From biological point of view, the notation $\varphi_i(t; t_0, s_0)$ in definition 2.1 means the size of individuals of the ith population at the moment t, which is s_0 at the moment t_0, and $R_i(P_1, P_2)$ $(i = 1, 2)$ in Eq. (3.18) denotes the physiological reproductive value of the individuals of the ith species, that is the number of offspring of each individual of the ith species during its lifetime with intraspecific and interspecific competition. Ecologically any individual of a species experiences some intraspecific regulatory negative feedback, besides, if a species is faced with an interference competition from another species, this interaction also will have a negative effect on the reproductive value. Mathematically speaking, that means $\frac{\partial R_i}{\partial P_j} < 0, \ i, j = 1, 2$. Thus the condition $R_i(0, 0) > 1$ is necessary for the coexistence of the two species, for if $R_i(0, 0) \leq 1$, then there cannot be positive pair that satisfies Eq. (3.18).

Moreover, within the framework presented here, multi-species models such as ($i = 1, 2, \cdots, n$)

$$\frac{\partial p_i(s,t)}{\partial t} + \frac{\partial(g_i(s, P_1(t), \cdots, P_n(t))p_i(s,t))}{\partial s} = -\mu_i(s, P_1(t), \cdots, P_n(t))p_i(s,t) \ ,$$

$$g_i(0, P_1(t), \cdots, P_n(t))p_i(0,t) = \int_0^\infty \beta_i(s, P_1(t), \cdots, P_n(t))p_i(s,t)\mathrm{d}s \ ,$$

$$p_i(s,0) = p_{i0}(s) \ ,$$

can be treated similarly. Of course, theoretical analysis will be more complicated.

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[1]Department of Mathematics, China Jiliang University, Hangzhou 310018, China.

Email: yliu@cjlu.edu.cn

[2]Institute of Operational Research and Cybernetics, Hangzhou Dianzi University, Hangzhou 310018, China.

Email: zrhe@hdu.edu.cn