Available online at www.sciencedirect.com

ScienceDirect

J. Differential Equations 260 (2016) 5926–5955

Journal of Differential Equations

www.elsevier.com/locate/jde

Global dynamics of delay equations for populations with competition among immature individuals

Eduardo Liz *, Alfonso Ruiz-Herrera

Departamento de Matemática Aplicada II, Universidad de Vigo, 36310 Vigo, Spain

Received 1 June 2015; revised 1 December 2015

Available online 28 December 2015

Abstract

We analyze a population model for two age-structured species allowing for inter- and intra-specific competition at immature life stages. The dynamics is governed by a system of Delay Differential Equations (DDEs) recently introduced by Gourley and Liu. The analysis of this model presents serious difficulties because the right-hand sides of the DDEs depend on the solutions of a system of nonlinear ODEs, and generally cannot be solved explicitly. Using the notion of strong attractor, we reduce the study of the attracting properties of the equilibria of the DDEs to the analysis of a related two-dimensional discrete system. Then, we combine some tools for monotone planar maps and planar competing Lotka–Volterra systems to describe the dynamics of the model with three different birth rate functions. We give easily verifiable conditions for global extinction of one or the two species, and for global convergence of the positive solutions to a coexistence state.

MSC: 34K20; 34A34; 39A10; 92D25

Keywords: Age structured population; Competition; Delay differential equations; Global attractor; Monotone planar maps; Lotka–Volterra systems

* Corresponding author. Fax: +34 986 818626.
E-mail addresses: eliz@dma.uvigo.es (E. Liz), alfonsoruiz@dma.uvigo.es (A. Ruiz-Herrera).

http://dx.doi.org/10.1016/j.jde.2015.12.020
0022-0396/

1. Introduction

Severe crowding or limited food resources are typical biological causes of inter- and intra-specific competition among species sharing the same habitat. In species with different age stages, it is broadly accepted that any type of competition usually takes place for the whole life-cycle, not only during the adult stage. In insect populations, specially in invasive species, the larval competition is well documented in many species and has deep biological consequences [1,2,4,12]. For instance, interspecific resource competition has been proposed as the most obvious explanation of the observed strong decline in the density of population of mosquitoes *Aedes aegypti* in the United States after the invasion of *Aedes albopictus* [17].

Despite the doubtless role of larval competition in real situations, most of commonly used mathematical models do not incorporate this phenomenon. Recently, Gourley and Liu have derived a system of delay differential equations which is a suitable model for species that experience immature life stage competition (see [5] and Section 2 below). In these models, the effect of competition at immature stages can be difficult to quantify because the right-hand sides of the delay equations cannot be defined explicitly. However, by applying some monotonicity results from [8], the authors derived a nice exclusion principle for the competition between two species: either there is a coexistence steady state or all nonnegative solutions with nonzero initial data converge to a semi-trivial equilibrium (see [5, Theorem 4.3]). Two possible drawbacks of this result are that the dynamics of the solutions is not known when there is a coexistence state, and that verifying whether coexistence states exist may not be an easy task due to the complexity of the nonlinearities involved in the models. These two limitations lessen the biological understanding of the role played by immature competition in particular situations.

In this paper we aim to provide a thorough analysis of some mathematical models with two species which incorporate intra- and inter-specific competition at immature life stages. For the considered models, we give easily verifiable conditions, involving the relevant biological parameters, for global extinction of one or the two species, or for global convergence to a coexistence state. Our analysis reveals that competition during juvenile stages potentially impacts the evolution of each species by affecting growth and survivorship, essentially in the same manner as adult competition do. As we shall show, in a scenario with only adult competition in which a particular species survives and the other one is doomed to extinction, the introduction of competition at larvae stages can be able to reverse this situation or give rise to a nontrivial global attractor where both species coexist in the long term.

Our approach is new and combines two main ingredients: First, the analysis of the competitive systems of delay differential equations introduced in [5] is reduced to the study of the dynamics of a related finite-dimensional discrete system. This reduction is based on the concept of strong attractor that we have introduced in [14]. Second, for usual birth rates (linear growth, Beverton–Holt and Ricker type nonlinearities), we construct a suitable system of ordinary differential equations of Lotka–Volterra type with time periodic coefficients to infer global dynamical properties in the system of delay differential equations. An advantage of our approach in comparison with [8,21] is that we apply some powerful tools from low dimensional dynamical systems to systems of delay differential equations, where the natural phase space is infinite-dimensional, and, in this way, we can prove sharper results; for instance, combining the notion of carrying simplex developed in [6] (see also [19]), and some subtle results on real analytic functions from [16,18], we can deduce that permanence of two competing species implies the existence of an isolated equilibrium which is a local attractor. Of course, the abstract results in ordered Banach spaces from [8,21] are more general and apply to a broad range of problems, beyond delay differential equations.

The paper is organized as follows: In Section 2 we introduce the system of DDEs developed in [5] and recall some details of the model formulation. In Section 3 we provide the theoretical background for our analysis. Finally, in Sections 4, 5, and 6, we present our main results for the global dynamics of the system of DDEs for the three aforementioned birth rates.

2. Competition between two species and age structured population models

It is well known that age-structured models can be reduced to delay differential equations (DDEs). Assuming a population divided into juvenile (immature) and adult (mature) life stages, Gourley and Liu [5] have recently derived a mathematical model for two populations subject to intra- and inter-specific competition between juveniles. For convenience of the reader, we recall some details to make clear the elements involved in the model formulation.

Consider two species structured by age groups and denote by $u_i(t,a)$ the density of individuals of the i-th species of age a at time t. In each species there are two age groups determined by a threshold $\tau > 0$ in which the sexual activity starts. For $0 < a < \tau$, the evolution of the immature individuals of those species is given by the age structured equations

$$\begin{aligned} \frac{\partial u_1(t,a)}{\partial t} + \frac{\partial u_1(t,a)}{\partial a} &= -c_1 u_1(t,a) - b_{11} u_1(t,a)^2 - b_{12} u_1(t,a) u_2(t,a), \\ \frac{\partial u_2(t,a)}{\partial t} + \frac{\partial u_2(t,a)}{\partial a} &= -c_2 u_2(t,a) - b_{21} u_1(t,a) u_2(t,a) - b_{22} u_2(t,a)^2. \end{aligned} \tag{2.1}$$

System (2.1) includes inter- and intra-specific competition between the species. Specifically, c_i and b_{ii} represent the death rate and the intra-specific competition between juveniles of the i-th species, respectively, while coefficients b_{ij} model inter-specific competition between immature individuals of the two species.

The age structured equations for adults ($a > \tau$) are

$$\frac{\partial u_1(t,a)}{\partial t} + \frac{\partial u_1(t,a)}{\partial a} = -\mu_1 u_1(t,a), \tag{2.2}$$

$$\frac{\partial u_2(t,a)}{\partial t} + \frac{\partial u_2(t,a)}{\partial a} = -\mu_2 u_2(t,a), \tag{2.3}$$

where μ_i is the per-capita mortality rate for the adults of the i-th species.

Denote by $u_i(t)$ the total mature population of the i-th species, i.e.,

$$u_i(t) = \int_\tau^\infty u_i(t,a)da. \tag{2.4}$$

Assuming that the birth rates depend on the total number of adults of the two species, we have

$$u_1(t,0) = b_1(u_1(t), u_2(t)), \quad u_2(t,0) = b_2(u_1(t), u_2(t)). \tag{2.5}$$

A suitable choice of the birth functions b_i allows to consider intra- and inter-specific competition at the adult level. If adults of the two species share the same (limited) food resources, then an increase in the number of individuals of the i-th species will reduce the chances of finding an adequate food supply within the j-th species. On the other hand, if the adult populations consume different food resources or food resources are unlimited, then the competition only occurs between immature populations.

After some steps, see Section 4 in [5] for details, the following system of DDEs is obtained for the evolution of $u_1(t)$ and $u_2(t)$:

$$\begin{aligned} u_1'(t) &= P_1(b_1(u_1(t-\tau), u_2(t-\tau)), b_2(u_1(t-\tau), u_2(t-\tau))) - \mu_1 u_1(t), \\ u_2'(t) &= P_2(b_1(u_1(t-\tau), u_2(t-\tau)), b_2(u_1(t-\tau), u_2(t-\tau))) - \mu_2 u_2(t), \end{aligned} \tag{2.6}$$

subject to nonnegative initial conditions $(u_1(s), u_2(s)) = (\phi_1(s), \phi_2(s))$, $s \in [-\tau, 0]$. Here,

$$\begin{aligned} P = (P_1, P_2) : \mathbb{R}^2_+ &\longrightarrow \mathbb{R}^2_+ \\ (x_0, y_0) &\mapsto (x_1(\tau; (x_0, y_0)), x_2(\tau; (x_0, y_0))) \end{aligned}$$

denotes the Poincaré map at time $\tau > 0$ of the system of ordinary differential equations

$$\begin{aligned} x_1'(t) &= -c_1 x_1(t) - b_{11}(x_1(t))^2 - b_{12} x_1(t) x_2(t), \\ x_2'(t) &= -c_2 x_2(t) - b_{21} x_2(t) x_1(t) - b_{22}(x_2(t))^2. \end{aligned} \tag{2.7}$$

The natural phase-space for (2.6) is $X = C([-\tau, 0], \mathbb{R}^2_+)$, equipped with the max-norm

$$|\phi|_\infty = \max\{|\phi_i(t)| : t \in [-\tau, 0]\},$$

where $\phi(t) = (\phi_1(t), \phi_2(t))$. For each $\phi \in X$, we employ the notation $(u_1(t; \phi), u_2(t; \phi))$ for the solution of (2.6) with initial condition ϕ. On the other hand, $(x_1(t; (x_0, y_0)), x_2(t; (x_0, y_0)))$ denotes the solution of (2.7) with initial condition $(x_0, y_0) \in \mathbb{R}^2_+$.

As noted in [5], although in general function P is not defined explicitly, if there is only one population and no intra-specific competition at immature stages ($u_2(t) \equiv 0$, $b_{11} = b_{12} = 0$), then system (2.6) becomes a well-known DDE which includes classical models as the Nicholson's blowflies equation or the Mackey–Glass equation.

3. Strong attractors and monotone systems

The aim of this section is to relate the study of a planar system of delay differential equations

$$\begin{aligned} x_1'(t) &= F_1(x_1(t-\tau_1), x_2(t-\tau_2)) - \mu_1 x_1(t), \\ x_2'(t) &= F_2(x_1(t-\tau_3), x_2(t-\tau_4)) - \mu_2 x_2(t), \end{aligned} \tag{3.1}$$

with the dynamics of an associated system of difference equations via the notion of strong attractor developed in [14] when $F = (F_1, F_2)$ enjoys some suitable monotone conditions. In Section 3.1, we recall and extend some concepts and results from [14], and in Section 3.2 we give some sufficient conditions to have strong attractors in the context of system (2.6).

3.1. Background on strong attractors

For convenience of the reader, we recall the notion of strong attractor and the main result from [14], applied to system (3.1).

Definition 3.1. Let $F : D \subset \mathbb{R}^2 \longrightarrow D$ be a continuous map defined on $D = (a_1, b_1) \times (a_2, b_2)$. An equilibrium $z_* \in D$ of the system

$$x(N+1) = F(x(N)), \quad N = 0, 1, 2, \dots$$

is a strong attractor in D if for every compact set $K \subset D$ there exists a family of sets $\{I_n\}_{n\in\mathbb{N}}$ where I_n is the product of s compact intervals satisfying that

(H1) $K \subset \mathrm{Int} I_1 \subset D$,
(H2) $F(I_n) \subset I_{n+1} \subset \mathrm{Int} I_n$ for all $n \in \mathbb{N}$,
(H3) $z_* \in \mathrm{Int} I_n$ for all $n \in \mathbb{N}$ and $\bigcap_{n=1}^{\infty} I_n = \{z_*\}$.

As before, for $\phi \in \mathcal{C}([-\tau, 0), \mathbb{R}^2)$, we employ the notation $x(t, \phi) = (x_1(t, \phi), x_2(t, \phi))$ for the solution of (3.1) with initial condition ϕ. Here, $\tau = \max\{\tau_i : i = 1, 2, 3, 4\}$.

The main result in [14] relates the notion of strong attractor with global attraction in (3.1); Theorem 3.1 below is a consequence of Theorem 2.5 and Remark 2.2 in [14].

Theorem 3.1. *Assume that $G := (\frac{1}{\mu_1} F_1, \frac{1}{\mu_2} F_2) : D \subset \mathbb{R}^2 \longrightarrow D$ is a locally Lipschitz-continuous map defined on $D = (a_1, b_1) \times (a_2, b_2)$, and $z_* \in \mathbb{R}^2$ is a strong attractor for*

$$x(N+1) = G(x(N)) \quad N = 0, 1, \dots \tag{3.2}$$

in D. Then, for each $\phi \in \{x \in \mathcal{C}([-\tau, 0], \mathbb{R}^2) : x(t) \in D \text{ for all } t \in [-\tau, 0]\}$,

$$\lim_{t\to\infty} x(t, \phi) = z_*.$$

Remark 3.1. Fix $K \subset D$ a compact set and $\{I_n\}$ the corresponding sequence given in Definition 3.1. From the proof of Theorem 2.5 in [14] it is clear that for each initial condition ϕ and $n \in \mathbb{N}$, there is $t_n > 0$ so that $x(t, \phi) \in I_n$ for all $t \geq t_n$.

Next we provide some variants of Theorem 3.1 for system (3.1). The proofs of Theorems 3.2 and 3.3 below are completely analogous to the proof of Theorem 3.1, so we omit them.

Definition 3.2. Let $F = (F_1, F_2) : \mathbb{R}^2_+ \longrightarrow \mathbb{R}^2_+$ be a continuous map. The set $[0, a] \times [0, b]$ is a strong attractor set in $\mathbb{R}^2_+$ if for every compact set $K \subset \mathbb{R}^2_+$, there is a family $\{I_n\}$ of products of two compact intervals with the following properties:

(H1′) $K \subset \mathrm{Int}_{\mathbb{R}^2_+} I_1$,
(H2′) $F(I_n) \subset I_{n+1} \subset \mathrm{Int}_{\mathbb{R}^2_+} I_n$ for all $n \in \mathbb{N}$,
(H3′) $[0, a] \times [0, b] \subset \mathrm{Int}_{\mathbb{R}^2_+} I_n$ and $\bigcap_{n=1}^{\infty} I_n = [0, a] \times [0, b]$.

Theorem 3.2. *Assume that* $G = \left(\frac{F_1}{\mu_1}, \frac{F_2}{\mu_2}\right) : \mathbb{R}^2_+ \longrightarrow \mathbb{R}^2_+$ *is locally Lipschitz-continuous and* $[0, a] \times [0, b]$ *is a strong attractor set for* G *in* $\mathbb{R}^2_+$. *Fix any compact set* K *and* $\{I_n\}$ *the corresponding family of Definition 3.2. Then, for each* $\phi \in \{x \in \mathcal{C}([-\tau, 0], \mathbb{R}^2) : x(t) \in K$ *for all* $t \in [-\tau, 0]\}$ *and* $n \in \mathbb{N}$, *there is* $t_n > 0$ *so that* $x(t; \phi) \in I_n$ *for all* $t \geq t_n$. *Moreover,* $\omega(\phi) \subset [0, a] \times [0, b]$.

We write $\mathrm{Int}_{\mathbb{R}^2_+}(A)$ to denote the interior of A relative to $\mathbb{R}^2_+$, and $\omega(\phi)$ for the usual omega limit set of the solution of (3.1) with initial condition ϕ.

Definition 3.3. Let $F : (a, b) \times [0, c) := D \subset \mathbb{R}^2_+ \longrightarrow (a, b) \times [0, c)$ be a continuous map. An equilibrium $(x_*, 0) \in D$ of the system

$$x(N + 1) = F(x(N)), \quad N = 0, 1, 2, \ldots$$

is a boundary strong attractor in D if for every compact set $K \subset D$ there exists a family of sets $\{I_n\}_{n\in\mathbb{N}}$ where I_n is the product of two compact intervals satisfying that

(H1″) $K \subset \mathrm{Int}_{\mathbb{R}^2_+} I_1 \subset D$,
(H2″) $F(I_n) \subset I_{n+1} \subset \mathrm{Int}_{\mathbb{R}^2_+} I_n$ for all $n \in \mathbb{N}$,
(H3″) $(x_*, 0) \in \mathrm{Int}_{\mathbb{R}^2_+} I_n$ for all $n \in \mathbb{N}$ and $\bigcap_{n=1}^{\infty} I_n = \{(x_*, 0)\}$.

Theorem 3.3. *Assume that* $G = \left(\frac{F_1}{\mu_1}, \frac{F_2}{\mu_2}\right) : D \subset \mathbb{R}^2_+ \longrightarrow D$ *is locally Lipschitz-continuous.*

(a) *If* $D = (a, b) \times [0, c)$, *and* $(x_*, 0) \in \mathbb{R}^2_+$ *is a boundary strong attractor for (3.2) in* D, *then*

$$\lim_{t\to\infty} x(t, \phi) = (x_*, 0),$$

for each $\phi \in \{x \in \mathcal{C}([-\tau, 0], \mathbb{R}^2) : x(t) \in D$ *for all* $t \in [-\tau, 0]\}$.

(b) *If* $D = [0, c) \times (a, b)$, *and* $(0, y_*) \in \mathbb{R}^2_+$ *is a boundary strong attractor for (3.2) in* D, *then*

$$\lim_{t\to\infty} x(t, \phi) = (0, y_*),$$

for each $\phi \in \{x \in \mathcal{C}([-\tau, 0], \mathbb{R}^2) : x(t) \in D$ *for all* $t \in [-\tau, 0]\}$.

3.2. Strong attractors in monotone systems

In this section, we consider the "south-east ordering" in $\mathbb{R}^2$, that is, the partial order $\preceq$ generated by the closed fourth quadrant in $\mathbb{R}^2$: given $(x_0, y_0), (x_1, y_1) \in \mathbb{R}^2$, $(x_0, y_0) \preceq (x_1, y_1)$ if $x_0 \leq x_1$ and $y_1 \leq y_0$. As usual, we also write $(x_0, y_0) < (x_1, y_1)$ if $(x_0, y_0) \preceq (x_1, y_1)$ and $(x_0, y_0) \neq (x_1, y_1)$, and $(x_0, y_0) \ll (x_1, y_1)$ if $x_0 < x_1$ and $y_1 < y_0$. If $z_0 = (x_0, y_0), z_1 = (x_1, y_1) \in \mathbb{R}^2$ and $z_0 \preceq z_1$, then the order interval generated by z_0 and z_1 is the set

$$[z_0, z_1] := \{z \in \mathbb{R}^2 : z_0 \preceq z \preceq z_1\}.$$

Notice that $[z_0, z_1]$ is a product of two real intervals, namely $[z_0, z_1] = [x_0, x_1] \times [y_1, y_0]$.

We recall that a continuous map $F = (F_1, F_2) : \mathbb{R}^2_+ \longrightarrow \mathbb{R}^2_+$ is order-preserving or monotone if $z_0 \preceq z_1$ implies $F(z_0) \preceq F(z_1)$. Following [20], a map F which is monotone with respect to the south-east ordering is called competitive. The map F is strongly monotone if $z_0 < z_1$ implies $F(z_0) \ll F(z_1)$. Following [6], we say that F is strictly retrotone if $F_1(x, y) \le F_1(\widetilde{x}, \widetilde{y})$, $F_2(x, y) \le F_2(\widetilde{x}, \widetilde{y})$, with $F(x, y) \ne F(\widetilde{x}, \widetilde{y})$, imply $x < \widetilde{x}$ if $\widetilde{x} \ne 0$, and $y < \widetilde{y}$ if $\widetilde{y} \ne 0$.

Consider the discrete system

$$\begin{aligned} x_{n+1} &= x_n f_1(x_n, y_n), \quad n \ge 0, \\ y_{n+1} &= y_n f_2(x_n, y_n), \quad n \ge 0, \end{aligned} \tag{3.3}$$

with f_i strictly positive, and define the map

$$\begin{aligned} F = (F_1, F_2) : \mathbb{R}^2_+ &\longrightarrow \mathbb{R}^2_+ \\ (x, y) &\mapsto (x f_1(x, y), y f_2(x, y)). \end{aligned}$$

We assume that F is of class $\mathcal{C}^1$ and we list the following conditions for later use:

(S1) $F(\mathbb{R}^2_+) \subset [0, \alpha) \times [0, \beta)$, for some $\alpha > 0$, $\beta > 0$.

(S2) $f_1(x, 0)$, $f_2(0, y)$ are strictly decreasing and $h_1(x) = x f_1(x, 0)$, $h_2(y) = y f_2(0, y)$ are strictly increasing provided $0 \le x < \alpha$ and $0 \le y < \beta$.

(S3) For all $(x, y) \in (0, \alpha) \times (0, \beta)$,

$$F'(x, y) = \begin{pmatrix} + & - \\ - & + \end{pmatrix}.$$

With these properties, the set $J = [0, \alpha) \times [0, \beta)$ is F-invariant and F is monotone in J. Moreover, if $z < \widetilde{z}$ and $z, \widetilde{z}$ are not on the same coordinate-axis then $F(z) \ll F(\widetilde{z})$. In particular, F is strongly monotone in the interior of J. These remarks will allow us to apply the convergence results for competitive maps established in [20, Section 5].

A fixed point $(\widetilde{x}, \widetilde{y})$ of F with $\widetilde{x} \ne 0$ (resp. $\widetilde{y} \ne 0$) satisfies that $f_1(\widetilde{x}, \widetilde{y}) = 1$ (resp. $f_2(\widetilde{x}, \widetilde{y}) = 1$). Thus, by **(S2)**, the map F has a semi-trivial equilibrium in the x-axis or the y-axis if and only if $f_1(0, 0) > 1$ or $f_2(0, 0) > 1$, respectively. For convenience in our exposition, we sometimes use the additional condition

(S4) $f_1(0, 0) > 1$ and $f_2(0, 0) > 1$.

Some examples of maps satisfying conditions **(S1)–(S3)**, and usually employed in discrete population models, are $F(x, y) = (c_1 x/(1 + x + y), c_2 y/(1 + x + y))$ with $c_i > 0$, and $G(x, y) = (x e^{r_1 - a_{11}x - a_{12}y}, y e^{r_2 - a_{21}x - a_{22}y})$ with $0 < r_i < 1$ and $a_{ij} > 0$ for $i, j = 1, 2$ (see, e.g., [20]).

Other map that fulfills conditions **(S1)–(S3)** is the Poincaré map $P = (P_1, P_2)$ at time $\tau > 0$ of the competitive system

$$\begin{aligned} x_1' &= x_1(c_1 - b_{11}x_1 - b_{12}x_2), \\ x_2' &= x_2(c_2 - b_{21}x_1 - b_{22}x_2), \end{aligned} \tag{3.4}$$

with $b_{ij} > 0$ for $i, j = 1, 2$.

To check that P is bounded, note that

$$P_i(u_1, u_2) \le \widetilde{P}_i(u_i),$$

for all $(u_1, u_2) \in \mathbb{R}^2_+$, where $\widetilde{P}_i$ is the Poincaré map at time τ of the scalar equation

$$x_i' = -c_i x_i - b_{ii} x_i^2.$$

By simple integration, $\widetilde{P}_i(u_i) = u_i h_i(u_i)$ is strictly increasing, with h_i positive and strictly decreasing. Moreover,

$$\lim_{u_i \to \infty} \widetilde{P}_i(u_i) < \infty. \tag{3.5}$$

The following lemmas provide some useful properties:

Lemma 3.1. *If P denotes the Poincaré map of (3.4), then for $H(x, y) = (p_1 x, p_2 y)$ and $G(x, y) = (r_1 x, r_2 y)$ with all parameters positive, $\Delta = H \circ P \circ G$ satisfies conditions* **(S1)–(S3)** *for suitable α, β.*

Proof. Denote $P(x, y) = (x f_1(x, y), y f_2(x, y))$. Then,

$$\Delta(x, y) = (x d_1(x, y), y d_2(x, y)),$$

with $d_i(x, y) = p_i r_i f_i(r_1 x, r_2 y)$, $i = 1, 2$.

We know that P satisfies properties **(S2)–(S3)** for any positive value of α and β. Thus, **(S2)–(S3)** also hold for Δ with any value of α and β. Since, by (3.5), P is bounded, condition **(S1)** holds choosing α and β such that $P(\mathbb{R}^2_+) \subset [0, \alpha/(p_1 r_1)) \times [0, \beta/(p_2 r_2))$. □

Lemma 3.2. *Assume that G satisfies properties* **(S1)–(S3)**. *If F satisfies* **(S2)–(S3)** *with the same α, β, and $F([0, \alpha) \times [0, \beta)) \subset [0, \alpha) \times [0, \beta)$, then $F \circ G$ satisfies conditions* **(S1)–(S3)**.

The following result shows that, under some additional assumptions, an isolated positive attractor of F is a strong attractor.

Theorem 3.4. *Assume that F satisfies* **(S1)–(S4)** *and*

- **(C1)** $\det(F'(x, y)) > 0$ *for all $(x, y) \in J = [0, \alpha) \times [0, \beta)$.*
- **(C2)** *If $(x_1, y_1), (x_2, y_2) \in J$ so that $F_1(x_1, y_1) \le F_1(x_2, y_2)$ and $F_2(x_1, y_1) \le F_2(x_2, y_2)$ with $F(x_1, y_1) \ne F(x_2, y_2)$, then $f_1(x_1, y_1) > f_1(x_2, y_2)$ if $x_2 \ne 0$, and $f_2(x_1, y_1) > f_2(x_2, y_2)$ if $y_2 \ne 0$.*

If $(\widetilde{x}, \widetilde{y}) \in \mathrm{Int}\mathbb{R}^2_+$ is an isolated local attractor of F, then $(\widetilde{x}, \widetilde{y})$ is a strong attractor of F in some neighbourhood of $(\widetilde{x}, \widetilde{y})$. This neighbourhood is determined by the positive fixed points of F.

Proof. Denote by $(x_*, 0)$ and $(0, y_*)$ the semi-trivial equilibria of F. Notice that the existence of those points is ensured by **(S4)**, and $0 < x_* < \alpha$, $0 < y_* < \beta$.

Since $\det F'(x, y) > 0$ for all $(x, y) \in J$, we deduce that F is locally injective and, by **(C1)**, **(S3)**,

$$(F')^{-1}(x, y) = \begin{pmatrix} + & + \\ + & + \end{pmatrix},$$

for all $(x, y) \in (0, \alpha) \times (0, \beta)$. Then, the conditions of Theorem 6.1 in [19] hold. Indeed, the first condition of Theorem 6.1 follows from **(S4)**. Next, F is strictly retrotone by Proposition 4.1 in [19]. Finally, the third condition of Theorem 6.1 is exactly **(C2)**. As a consequence, F has a so-called carrying simplex (see [6,11]), that is to say, there is an F-invariant curve γ with the following properties:

(CS1) γ is homeomorphic to $[0, x_*]$,
(CS2) γ is totally balanced, i.e. if $(x_1, y_1), (x_2, y_2) \in \gamma$ with $x_1 \le y_1$ and $x_2 \le y_2$ then $(x_1, y_1) = (x_2, y_2)$,
(CS3) for every $z = (x(0), y(0)) \in \mathbb{R}^2_+ \backslash \{(0, 0)\}$, there exists $\widetilde{z} \in \gamma$ so that

$$\lim_{N\to\infty} [F^N(\widetilde{z}) - F^N(z)] = 0,$$

(CS4) $F|_\gamma : \gamma \longrightarrow \gamma$ is a homeomorphism.

By these properties, γ contains all nontrivial equilibria of F since by **(CS3)** and the invariance of the axes and γ under F, γ must contain $(x_*, 0)$ and $(0, y_*)$. By **(CS2)**, $p : \gamma \longrightarrow [0, x_*]$ given by $p(x, y) = x$ defines a homeomorphism. Thus $g = p \circ F|_\gamma \circ p^{-1} : [0, x_*] \longrightarrow [0, x_*]$ is injective. Note that $g(x) = F_1(x, p^{-1}(x))$ where $p^{-1}(x)$ is the unique point satisfying that $(x, p^{-1}(x)) \in \gamma$. As $(\widetilde{x}, \widetilde{y})$ is an isolated local attractor of F, we have that $\widetilde{x}$ is an isolated attractor for g. Since $g(0) = 0$ and g is injective, g is strictly increasing. Hence, since $\widetilde{x}$ is an isolated attractor for g, there are two points x_0, $\widetilde{x}_0$ such that $x_0 < \widetilde{x} < \widetilde{x}_0$, $g^n(x) \nearrow \widetilde{x}$ for all $x \in (x_0, \widetilde{x})$ and $g^n(\widetilde{x}) \searrow \widetilde{x}$ for all $x \in (\widetilde{x}, \widetilde{x}_0)$. Moreover, we can choose $\widetilde{x}_0$ as the minimum of the fixed points of g greater than $\widetilde{x}$ and x_0 the maximum of the fixed points of g smaller than $\widetilde{x}$.

Next we prove that $(\widetilde{x}, \widetilde{y})$ is a strong attractor of F in

$$\mathrm{Int}[(x_0, y_0), (\widetilde{x}_0, \widetilde{y}_0)] = (x_0, \widetilde{x}_0) \times (\widetilde{y}_0, y_0),$$

where $p^{-1}(x_0) = (x_0, y_0) \in \gamma$ and $p^{-1}(\widetilde{x}_0) = (\widetilde{x}_0, \widetilde{y}_0) \in \gamma$. Fix $K \subset \mathrm{Int}[(x_0, y_0), (\widetilde{x}_0, \widetilde{y}_0)]$ a compact set. Take $x \in (x_0, \widetilde{x})$ and $X \in (\widetilde{x}_0, \widetilde{x})$ so that

$$K \subset \mathrm{Int}[(x, p^{-1}(x)), (X, p^{-1}(X))] := I_1.$$

Since F is monotone in J and I_1 is an order interval, it follows that

$$F(I_1) \subset [F(x, p^{-1}(x)), F(X, p^{-1}(X))].$$

Next, by **(CS2)**, $F(x, p^{-1}(x)) \gg (x, p^{-1}(x))$ and $F(X, p^{-1}(X)) \ll (X, p^{-1}(X))$. Hence,

$$F(I_1) \subset I_2 := [F(x, p^{-1}(x)), F(X, p^{-1}(X))] \subset \mathrm{Int} I_1,$$

and $(\widetilde{x}, \widetilde{y}) \in \mathrm{Int} I_2$. In an inductive way, as $\{F^n(x, p^{-1}(x))\}, \{F^n(X, p^{-1}(X))\}$ tend to $(\widetilde{x}, \widetilde{y})$, the family of intervals

$$I_n = [F^n(x, p^{-1}(x)), F^n(X, p^{-1}(X))]$$

satisfies the properties of Definition 3.1. $\square$

Remark 3.2. Notice that if $(\widetilde{x}, \widetilde{y})$ is the unique equilibrium of F in the interior of J then $(\widetilde{x}, \widetilde{y})$ is a strong attractor of F in $(0, x_*) \times (0, y_*)$.

The next lemma gives some useful properties to check conditions **(C1)–(C2)**.

Lemma 3.3. *Assume that F satisfies* **(S1)**, **(S3)** *and* **(C1)**. *If f_i is strictly decreasing in both components, $i = 1, 2$, then* **(C2)** *holds. Moreover, if F and G satisfy* **(S3)**, **(C1)** *and* **(C2)** *for any value of α and β, then the same properties hold for $F \circ G$.*

Proof. We first note that if a map satisfies **(S3)** and **(C1)** then it is strictly retrotone, see Proposition 4.1 in [19]. Next we prove the first statement of the lemma. Take $(x_1, y_1), (x_2, y_2)$ so that $F_1(x_1, y_1) = x_1 f_1(x_1, y_1) \le x_2 f_1(x_2, y_2) = F_1(x_2, y_2)$ and $y_1 f_2(x_1, y_1) = F_2(x_1, y_1) \le x_2 f_2(x_2, y_2) = F_2(x_2, y_2)$ with $F(x_1, y_1) \neq F(x_2, y_2)$. As F is strictly retrotone, we have that $x_1 < x_2$ if $x_2 \neq 0$ and $y_1 < y_2$ if $y_2 \neq 0$. Observe that $x_2 = 0$ implies $x_1 = 0$, and $y_2 = 0$ implies $y_1 = 0$. Now, if f_i is strictly decreasing in both components, clearly **(C2)** holds.

Next we prove the second claim of the lemma. Assume that $F \circ G = H = (H_1, H_2) = (x h_1(x, y), y h_2(x, y))$. It is clear that **(S3)** and **(C1)** hold for H. Take $(x_1, y_1), (x_2, y_2)$ so that $H_1(x_1, y_1) = x_1 h_1(x_1, y_1) \le x_2 h_1(x_2, y_2) = H_1(x_2, y_2)$ and $y_1 h_2(x_1, y_1) = H_2(x_1, y_1) \le x_2 h_2(x_2, y_2) = H_2(x_2, y_2)$ with $H(x_1, y_1) \neq H(x_2, y_2)$.

As F is strictly retrotone, we have that $G_1(x_1, y_1) < G_1(x_2, y_2)$ if $G_1(x_2, y_2) \neq 0$, and $G_2(x_1, y_1) < G_2(x_2, y_2)$ if $G_2(x_2, y_2) \neq 0$. Again, as G is strictly retrotone, we have that $x_1 < x_2$ if $x_2 \neq 0$, and $y_1 < y_2$ if $y_2 \neq 0$. Now we have by **(C2)** that if $x_2 \neq 0$, then

$$g_1(x_2, y_2) > g_1(x_1, y_1), \quad f_1(G((x_2, y_2)) > f_1(G((x_1, y_1)).$$

Finally, from these inequalities, we deduce that

$$h_1(x_2, y_2) = g_1(x_2, y_2) f_1(G((x_2, y_2)) > h_1(x_1, y_1) = g_1(x_1, y_1) f_1(G((x_1, y_1)). \qquad \square$$

The above given examples of maps satisfying properties **(S1)–(S3)** also satisfy **(C1)–(C2)**.

Proposition 3.1. *Assume that F satisfies* **(S1)–(S3)** *and $(x_*, 0)$, $(0, y_*)$ are global attractors of F on the x-axis and the y-axis, respectively. Then, the order interval $[(0, y_*), (x_*, 0)] = [0, x_*] \times [0, y_*]$ is a strong attractor set for F in $\mathbb{R}^2_+$.*

Proof. Fix $K \subset \mathbb{R}^2_+$ a compact set. Take $M > \max\{\alpha, \beta\}$ so that

$$K \subset [(0, M), (M, 0)] = [0, M] \times [0, M].$$

Next define the sequence $\{\alpha_n\}$ obtained from the iteration of the discrete equation

$$x_{n+1} = x_n f_1(x_n, 0), \quad n = 1, 2, \ldots,$$

with initial condition $\alpha_1 = \alpha$, and $\{\beta_n\}$ the sequence obtained from

$$y_{n+1} = y_n f_2(0, y_n), \quad n = 1, 2, \ldots,$$

with initial condition $\beta_1 = \beta$. The sequences

$$M_n = \begin{cases} M & \text{if} \quad n = 1 \\ \alpha_{n-1} & \text{if} \quad n > 1 \end{cases}$$

$$m_n = \begin{cases} M & \text{if} \quad n = 1 \\ \beta_{n-1} & \text{if} \quad n > 1 \end{cases}$$

are strictly decreasing and tend to x_* and y_*, respectively. Since $xf_1(x, 0)$ is strictly increasing in $(0, \alpha)$, $F_1(x, y) \leq \alpha$, for all $x \in [0, M]$, and **(S3)** holds, it follows that

$$F_1(x, y) \leq F_1(x, 0) \leq F_1(M_n, 0) = M_{n+1},$$

for all $x \in [0, M_n]$ and $y \in [0, m_n]$. Analogously,

$$F_2(x, y) \leq F_2(0, y) \leq F_2(0, m_n) = m_{n+1},$$

for all $x \in [0, M_n]$ and $y \in [0, m_n]$.

Now, it is straightforward to prove that the family of order intervals

$$I_n = [(0, m_n), (M_n, 0)] = [0, M_n] \times [0, m_n], \quad n = 1, 2, \ldots$$

satisfies properties **(H1′)**–**(H3′)** of Definition 3.2. Note that

$$F(I_n) \subset I_{n+1} \subset \mathrm{Int}_{\mathbb{R}^2_+} I_n, \ \forall n. \qquad \square$$

Proposition 3.2. *Assume that F satisfies* **(S1)**–**(S3)** *and $(x_*, 0)$, $(0, y_*)$ are global attractors of F on the x-axis and the y-axis, respectively.*

(a) Attraction to $(x_*, 0)$**.** *Suppose that $x_* > 0$, F has no fixed points in $\mathrm{Int}\mathbb{R}^2_+$, and $f_1(0, y_*) > 1$. Then, given any $\varepsilon > 0$ sufficiently small to ensure $f_1(0, y_* + \varepsilon) > 1$, $(x_*, 0)$ is a boundary strong attractor for F in $(0, \alpha) \times [0, y_* + \varepsilon)$.*

(b) Attraction to $(0, y_*)$**.** *Suppose that $y_* > 0$, F has no fixed points in $\mathrm{Int}\mathbb{R}^2_+$, and $f_2(x_*, 0) > 1$. Then, given any $\varepsilon > 0$ sufficiently small to ensure $f_2(x_* + \varepsilon, 0) > 1$, $(0, y_*)$ is a boundary strong attractor for F in $[0, x_* + \varepsilon) \times (0, \beta)$.*

Proof. We only prove statement **(a)**. By the expression of F and our assumptions, we have that $f_2(0, y_*) \leq 1$ ($f_2(0, y_*) = 1$ if $y_* > 0$), and $f_1(0, y_*) > 1$. Fix $K \subset (0, \alpha) \times [0, y_* + \varepsilon)$. By a simple continuity argument and **(S3)**, we obtain that there exist $\widetilde{\varepsilon} > 0$, $\delta > 0$, $M \in (x_*, \alpha)$ such that

$$K \subset [(\delta, y_* + \widetilde{\varepsilon}), (M, 0)] = [\delta, M] \times [0, y_* + \widetilde{\varepsilon}],$$

with $f_1(\delta, y_* + \widetilde{\varepsilon}) > 1$, $f_2(\delta, y_* + \widetilde{\varepsilon}) < 1$.

By these properties it is clear that $F(\delta, y_* + \widetilde{\varepsilon}) \gg (\delta, y_* + \widetilde{\varepsilon})$ and therefore, since F is strongly monotone in $(0, \alpha) \times (0, \beta)$, it follows that $F^n(\delta, y_* + \widetilde{\varepsilon}) \gg F^{n-1}(\delta, y_* + \widetilde{\varepsilon})$ for all $n \geq 1$. Moreover, by the attraction on the x-axis we have that $F^n(M, 0) \preceq F^{n-1}(M, 0)$ for all $n \geq 1$. Since both sequences $\{F^n(\delta, y_* + \widetilde{\varepsilon})\}$, $\{F^n(M, 0)\}$ tend to $(x_*, 0)$ (use [20, Theorem 5.2] for the former one), we conclude the result choosing the family of intervals $I_n = [F^n(\delta, y_* + \widetilde{\varepsilon}), F^n(M, 0)]$. $\square$

Proposition 3.3 *(Attraction to $(\widetilde{x}, \widetilde{y})$). Assume that F satisfies* **(S1)–(S4)** *and $(x_*, 0)$, $(0, y_*)$ are global attractors of F on the x-axis and the y-axis, respectively. In addition, suppose that $(0, 0)$, $(x_*, 0)$, $(0, y_*)$, $(\widetilde{x}, \widetilde{y})$ are the unique fixed points of F with $\widetilde{x} > 0$, $\widetilde{y} > 0$, and $f_1(0, y_*) > 1$, $f_2(x_*, 0) > 1$. Then given any $\varepsilon > 0$ sufficiently small to ensure $f_1(0, y_* + \varepsilon) > 1$, $f_2(x_* + \varepsilon, 0) > 1$, $(\widetilde{x}, \widetilde{y})$ is a strong attractor for F in $(0, x_* + \varepsilon) \times (0, y_* + \varepsilon)$.*

Proof. Fix $K \subset (0, x_* + \varepsilon) \times (0, y_* + \varepsilon)$ a compact set. Take $\delta, \widetilde{\varepsilon} > 0$ so that

$$K \subset [\delta, x_* + \widetilde{\varepsilon}] \times [\delta, y_* + \widetilde{\varepsilon}]$$

and

$$\begin{aligned} &f_1(x_* + \widetilde{\varepsilon}, \delta) < 1; \quad && f_2(x_* + \widetilde{\varepsilon}, \delta) > 1, \\ &f_1(\delta, y_* + \widetilde{\varepsilon}) > 1; \quad && f_2(\delta, y_* + \widetilde{\varepsilon}) < 1. \end{aligned}$$

By these inequalities, it is clear that $(\delta, y_* + \widetilde{\varepsilon}) \gg F(\delta, y_* + \widetilde{\varepsilon})$ and $(x_* + \widetilde{\varepsilon}, \delta) \ll F(x_* + \widetilde{\varepsilon}, \delta)$. Now, as F is strongly monotone in $(0, \alpha) \times (0, \beta)$, we have that $F^{n-1}(\delta, y_* + \widetilde{\varepsilon}) \gg F^n(\delta, y_* + \widetilde{\varepsilon})$ and $F^{n-1}(x_* + \widetilde{\varepsilon}, \delta) \ll F^n(x_* + \widetilde{\varepsilon}, \delta)$ for all $n \in \mathbb{N}$. Therefore, by [20, Theorem 5.3], the sequences $\{F^n(\delta, y_* + \widetilde{\varepsilon})\}$ and $\{F^n(x_* + \widetilde{\varepsilon}, \delta)\}$ tend to $(\widetilde{x}, \widetilde{y})$. Finally, define the sequence of intervals

$$I_n = [F^n(\delta, y_* + \widetilde{\varepsilon}), F^n(x_* + \widetilde{\varepsilon}, \delta)], \ n \geq 1.$$

We use that F is monotone to conclude that

$$F(I_n) \subset [F^n(\delta, y_* + \widetilde{\varepsilon}), F^n(x_* + \widetilde{\varepsilon}, \delta)] \subset \mathrm{Int} I_n, \ \forall n \in \mathbb{N}. \qquad \square$$

Remark 3.3. If we weaken the conditions of Proposition 3.3 to allow the existence of a finite number of fixed points of F in $\mathrm{Int}\mathbb{R}^2_+$, then we can deduce that $[z, \widetilde{z}]$ is a strong attractor set in $(0, x_* + \varepsilon) \times (0, y_* + \varepsilon)$ for suitable fixed points $z, \widetilde{z} \in \mathrm{Int}\mathbb{R}^2_+$.

Proposition 3.4. *Assume that F satisfies* **(S1)–(S4)** *and $(x_*, 0)$, $(0, y_*)$ are fixed points of F.*

(a) *If $f_2(x_*, 0) < 1$, then there exist constants $\delta > 0$, $\varepsilon > 0$ such that $(x_*, 0)$ is a boundary strong attractor of F in $(x_* - \delta, x_* + \delta) \times [0, \varepsilon)$.*

(b) *If $f_1(0, y_*) < 1$, then there exist constants $\delta > 0$, $\varepsilon > 0$ such that $(0, y_*)$ is a boundary strong attractor of F in $[0, \varepsilon) \times (y_* - \delta, y_* + \delta)$.*

Proof. We only prove **(a)** because the proof of **(b)** is analogous.

By a simple continuity argument, we can deduce that there exist $\delta > 0$, $\varepsilon > 0$ such that $f_1(x_* - \delta, \varepsilon) > 1$ and $f_2(x_* - \delta, \varepsilon) < 1$.

Take an arbitrary compact set K contained in $(x_* - \delta, x_* + \delta) \times [0, \varepsilon)$. We can find $\widetilde{\varepsilon}, \widetilde{\delta} > 0$ so that

$$K \subset [(x_* - \widetilde{\delta}, \widetilde{\varepsilon}), (x_* + \widetilde{\delta}, 0)] = [x_* - \widetilde{\delta}, x_* + \widetilde{\delta}] \times [0, \widetilde{\varepsilon}].$$

Arguing as in the proof of Proposition 3.2, it follows that the sequence of intervals

$$I_n = [F^n(x_* - \widetilde{\delta}, \widetilde{\varepsilon}), F^n(x_* + \widetilde{\delta}, 0)], \ n \in \mathbb{N},$$

satisfies the properties **(H1″)**–**(H3″)** of Definition 3.3. □

4. Dynamics of (2.6) under unlimited food resources during the adult stage

In this section we assume that the birth rates or egg-laying rates of the two species are given by $b_i(u_1, u_2) = p_i u_i$ with $p_i > 0$. This choice is natural when both species consume unlimited food resources during the adult stage. In this scenario, the competition only occurs at larval stages.

For convenience, we define $\Delta(u_1, u_2) = H \circ P \circ B(u_1, u_2)$ where $B(u_1, u_2) = (p_1 u_1, p_2 u_2)$, P is the Poincaré map introduced in section 2, and $H(u_1, u_2) = (\frac{u_1}{\mu_1}, \frac{u_2}{\mu_2})$. Δ can be written as

$$\Delta(u_1, u_2) = (u_1 h_1(u_1, u_2), u_2 h_2(u_1, u_2)), \tag{4.1}$$

with

$$\begin{aligned} &h_1(u_1, u_2) \\ &\quad = \frac{p_1}{\mu_1} \exp\left(-c_1\tau - b_{11}\int_0^\tau x_1(t; p_1u_1, p_2u_2)dt - b_{12}\int_0^\tau x_2(t; p_1u_1, p_2u_2)dt\right), \\ &h_2(u_1, u_2) \\ &\quad = \frac{p_2}{\mu_2} \exp\left(-c_2\tau - b_{21}\int_0^\tau x_1(t; p_1u_1, p_2u_2)dt - b_{22}\int_0^\tau x_2(t; p_1u_1, p_2u_2)dt\right). \end{aligned} \tag{4.2}$$

Here, we assume that $b_{ij} > 0$ for all $i, j = 1, 2$. In (4.2), $(x_1(t; p_1u_1, p_2u_2), x_2(t; p_1u_1, p_2u_2))$ denotes the solution of (2.7) with initial condition (p_1u_1, p_2u_2). By Lemma 3.1, Δ meets conditions **(S1)**–**(S3)** of Section 3.2 that we recall here in terms of Δ for the reader's convenience:

(S1) $\Delta(\mathbb{R}^2_+) \subset [0, \alpha) \times [0, \beta)$, for some $\alpha > 0$, $\beta > 0$.

(S2) $h_1(x, 0)$, $h_2(0, y)$ are strictly decreasing and $g_1(x) = x h_1(x, 0)$, $g_2(y) = y h_2(0, y)$ are strictly increasing provided $0 \le x < \alpha$ and $0 \le y < \beta$.

(S3) For all $(x, y) \in (0, \alpha) \times (0, \beta)$,

$$\Delta'(x, y) = \begin{pmatrix} + & - \\ - & + \end{pmatrix}.$$

The next results provide a thorough dynamical description of (2.6). There are two generic possibilities: either attraction to a unique equilibrium in $\mathrm{Int}\mathbb{R}^2_+$, or extinction of some species. We understand that an equilibrium (z_1, z_2) of (2.6) is an attractor in Ω if given an initial condition $(\phi_1(t), \phi_2(t))$ with $(\phi_1(t), \phi_2(t)) \in \Omega$ for all $t \in [-\tau, 0]$, $\lim_{t\to\infty} u_i(t, \phi_1, \phi_2) = z_i$, $i = 1, 2$. We omit Ω when we refer to $\mathrm{Int}\mathbb{R}^2_+$.

We define the numbers

$$A_i := h_i(0, 0) = \frac{p_i e^{-c_i\tau}}{\mu_i}, \quad i = 1, 2, \tag{4.3}$$

which are employed in the statements of the main results in this section.

Proposition 4.1. *Consider (2.6) with $b_i(u_1, u_2) = p_i u_i$, $i = 1, 2$.*

(i) *If $A_i \le 1$ for $i = 1, 2$, then $(0, 0)$ is a global attractor for (2.6).*
(ii) *If $A_1 > 1$ and $A_2 \le 1$, then there is $u_1^* > 0$ so that $(u_1^*, 0)$ is a global attractor for (2.6).*
(iii) *If $A_1 \le 1$ and $A_2 > 1$, then there is $u_2^* > 0$ so that $(0, u_2^*)$ is a global attractor for (2.6).*

Proof. By (4.3), if $A_i \le 1$ then $h_i(0, 0) \le 1$ for $i = 1, 2$. Hence, by **(S2)–(S3)**, given $(x, y) \in \mathrm{Int}\mathbb{R}^2_+$,

$$\Delta_1(x, y) \le \Delta_1(x, 0) < x,$$
$$\Delta_2(x, y) \le \Delta_2(0, y) < y,$$

and so $\mathrm{Fix}(\Delta) = \{(0, 0)\}$, where $\mathrm{Fix}(\Delta)$ denotes the set of fixed points of Δ. By Proposition 3.1, $\{(0, 0)\}$ is a strong attractor set for Δ in $\mathbb{R}^2_+$. Thus, statement (i) is a consequence of Theorem 3.2.

Next we prove (ii). If $A_1 > 1$ and $A_2 \le 1$, we have, by (4.3), that $h_1(0, 0) > 1$ and $h_2(0, 0) \le 1$. By **(S1)–(S3)** and a simple analysis, it follows that there is a unique $u_1^* > 0$ so that u_1^* is a global attractor of the difference equation

$$x_{n+1} = x_n h_1(x_n, 0), \quad n \ge 0.$$

On the other hand, $h_2(0, 0) \le 1$ implies that Δ has no fixed points in $\mathrm{Int}\mathbb{R}^2_+$, and 0 is a global attractor of

$$y_{n+1} = y_n h_2(0, y_n), \quad n \ge 0.$$

Now, take an initial condition $(\phi_1(t), \phi_2(t))$ with $\phi_i(t) > 0$ for all $t \in [-\tau, 0]$. We know that $h_1(0, 0) > 1$ and so, there is $\varepsilon > 0$ such that $h_1(0, \varepsilon) > 1$. Next, by Proposition 3.1 and Theorem 3.2, there is $t_* > 0$ so that $0 < u_1(t, \phi) < u_1^* + \varepsilon$ and $0 < u_2(t, \phi) < \varepsilon$ for all $t \ge t_*$. By Proposition 3.2, $(u_1^*, 0)$ is a boundary strong attractor for Δ in $D = (0, \alpha) \times [0, \varepsilon)$. Finally, we apply Theorem 3.3 to the initial condition $\psi(t) = (u_1(t + t_* + \tau, \phi), u_2(t + t_* + \tau, \phi)) \in D$,

$\forall t \in [-\tau, 0]$, to conclude that $\lim_{t\to\infty} x(t,\phi) = \lim_{t\to\infty} x(t,\psi) = (u_1^*, 0)$. The proof of (iii) is completely analogous. □

Remark 4.1. If $A_i > 1$ for $i = 1, 2$ then there are two fixed points of Δ, say $(u_1^*, 0)$ and $(0, u_2^*)$, and they are global attractors for the difference equations

$$x_{n+1} = x_n h_1(x_n, 0)$$

and

$$y_{n+1} = y_n h_2(0, y_n),$$

respectively.

Theorem 4.1. *Assume that $A_i > 1$ for $i = 1, 2$.*

- **i)** *If $\frac{\log A_1}{b_{11}} > \frac{\log A_2}{b_{21}}$ and $\frac{\log A_1}{b_{12}} > \frac{\log A_2}{b_{22}}$ then $(u_1^*, 0)$ is a global attractor of (2.6).*
- **ii)** *If $\frac{\log A_1}{b_{11}} < \frac{\log A_2}{b_{21}}$ and $\frac{\log A_1}{b_{12}} < \frac{\log A_2}{b_{22}}$ then $(0, u_2^*)$ is a global attractor of (2.6).*
- **iii)** *If $\frac{\log A_1}{b_{11}} > \frac{\log A_2}{b_{21}}$ and $\frac{\log A_1}{b_{12}} < \frac{\log A_2}{b_{22}}$ then $(u_1^*, 0)$ and $(0, u_2^*)$ are local attractors for (2.6).*
- **iv)** *If $\frac{\log A_1}{b_{11}} < \frac{\log A_2}{b_{21}}$ and $\frac{\log A_1}{b_{12}} > \frac{\log A_2}{b_{22}}$ then there is an equilibrium $(\widetilde{u}_1, \widetilde{u}_2) \in \mathrm{Int}\mathbb{R}^2_+$, and it is a global attractor of (2.6).*

Proof. First we note that a fixed point $(\widetilde{u}_1, \widetilde{u}_2) \in \mathrm{Int}\mathbb{R}^2_+$ of Δ satisfies the equations

$$\begin{aligned} \log A_1 &= b_{11}\int_0^\tau x_1(t; p_1\widetilde{u}_1, p_2\widetilde{u}_2)dt + b_{12}\int_0^\tau x_2(t; p_1\widetilde{u}_1, p_2\widetilde{u}_2)dt \\ \log A_2 &= b_{22}\int_0^\tau x_2(t; p_1\widetilde{u}_1, p_2\widetilde{u}_2)dt + b_{21}\int_0^\tau x_1(t; p_1\widetilde{u}_1, p_2\widetilde{u}_2)dt. \end{aligned} \tag{4.4}$$

Moreover, for the semi-trivial equilibria $(u_1^*, 0)$ and $(0, u_2^*)$, we get

$$\int_0^\tau x_1(t; p_1u_1^*, 0)dt = \frac{\log A_1}{b_{11}} \tag{4.5}$$

and

$$\int_0^\tau x_2(t; 0, p_2u_2^*)dt = \frac{\log A_2}{b_{22}}. \tag{4.6}$$

Now, given $(\phi_1(t), \phi_2(t))$ an initial condition with $\phi_i(t) > 0$ for all $t \in [-\tau, 0]$ and $\varepsilon > 0$, by Proposition 3.1 and Theorem 3.2, there is $t_* = t_*(\varepsilon) > 0$ so that

$$u_1(t,\phi(t)) \le u_1^* + \varepsilon, \quad u_2(t,\phi(t)) \le u_2^* + \varepsilon,$$

for all $t \ge t_*$.

Next, from (4.2), (4.5) and (4.6), we get the following equivalences:

$$\frac{\log A_1}{b_{12}} > \frac{\log A_2}{b_{22}} \Longleftrightarrow h_1(0,u_2^*) > 1; \quad \frac{\log A_1}{b_{11}} > \frac{\log A_2}{b_{21}} \Longleftrightarrow h_2(u_1^*,0) < 1. \tag{4.7}$$

These relations also hold if we reverse all the inequalities. As an example, we prove the first one: by (4.2),

$$h_1(0,u_2^*) = \frac{p_1}{\mu_1}\exp\left(-c_1\tau - b_{11}\int_0^\tau x_1(t;0,p_2u_2^*)dt - b_{12}\int_0^\tau x_2(t;0,p_2u_2^*)dt\right).$$

Since $x_1(t,0,p_2u_2^*) = 0$ and, by (4.6), $\int_0^\tau x_2(t;0,p_2u_2^*)dt = (\log A_2)/b_{22}$, we have

$$h_1(0,u_2^*) = A_1\exp\left(-\frac{b_{12}}{b_{22}}\log A_2\right) = \exp\left(-\frac{b_{12}}{b_{22}}\log A_2 + \log A_1\right).$$

Hence,

$$h_1(0,u_2^*) > 1 \Longleftrightarrow \log A_1 > \frac{b_{12}}{b_{22}}\log A_2 \Longleftrightarrow \frac{\log A_1}{b_{12}} > \frac{\log A_2}{b_{22}}.$$

Proof of i). It is clear that a necessary condition for the existence of fixed points of Δ in $\mathrm{Int}\mathbb{R}_+^2$ is that the linear system

$$\begin{aligned} \log A_1 &= b_{11}x + b_{12}y, \\ \log A_2 &= b_{22}y + b_{21}x, \end{aligned} \tag{4.8}$$

has a solution in $\mathrm{Int}\mathbb{R}_+^2$. By a geometrical analysis, one can see that under the conditions assumed in **i)**, (4.8) has no solution in $\mathrm{Int}\mathbb{R}_+^2$.

From (4.7), it follows that $h_1(0,u_2^*) > 1$, and therefore, by Proposition 3.2, $(u_1^*,0)$ is a boundary strong attractor for Δ in $D = (0,\alpha)\times[0,\varepsilon)$. Finally, as we did in the proof of Proposition 4.1, we apply Theorem 3.3 to the initial condition $\psi(t) = (u_1(t+t_*+\tau,\phi), u_2(t+t_*+\tau,\phi)) \in D$, $\forall t \in [-\tau,0]$, to conclude that $\lim_{t\to\infty} x(t,\phi) = \lim_{t\to\infty} x(t,\psi) = (u_1^*,0)$.

Proof of ii). This proof is completely analogous to the previous one.

Proof of iii). Under these conditions we have that $h_1(0,u_2^*) < 1$ and $h_2(u_1^*,0) < 1$, and the conclusion follows easily from Proposition 3.4 and Theorem 3.3.

Proof of iv). In this case, we have that $h_1(0,u_2^*) > 1$, $h_2(u_1^*,0) > 1$, $h_1(0,0) > 1$, and $h_2(0,0) > 1$. Moreover, Δ is bounded. These properties imply that the discrete system

$$x_{n+1} = \Delta_1(x_n, y_n),$$
$$y_{n+1} = \Delta_2(x_n, y_n),$$

is permanent. This conclusion can be carried out by applying Corollary 2.2 in [10] with functions $P(x, y) = x$ and $P(x, y) = y$ to prove that the axes are repellers for Δ. Hence, by Theorem 5 in [9], Δ has a fixed point in $\mathrm{Int}\mathbb{R}^2_+$, say $(\widetilde{u_1}, \widetilde{u_2})$. Next we prove that there is a unique fixed point of Δ in $\mathrm{Int}\mathbb{R}^2_+$. By contradiction, assume that $(\widetilde{\widetilde{u_1}}, \widetilde{\widetilde{u_2}})$ is a different fixed point of Δ. On the one hand, by **(S3)**, either $\widetilde{\widetilde{u_1}} < \widetilde{u_1}$ and $\widetilde{u_2} < \widetilde{\widetilde{u_2}}$, or $\widetilde{\widetilde{u_1}} > \widetilde{u_1}$ and $\widetilde{u_2} > \widetilde{\widetilde{u_2}}$. Moreover, the map

$$(t, u_1, u_2) \mapsto (x_1(t; p_1u_1, p_2u_2), x_2(t; p_1u_1, p_2u_2)),$$

where $(x_1(t, p_1u_1, p_2u_2), x_2(t, p_1u_1, p_2u_2))$ is the solution of (2.7) with initial condition (p_1u_1, p_2u_2), preserves the order induced by the fourth quadrant. Therefore, the inequalities

$$\int_0^\tau x_1(t; p_1\widetilde{\widetilde{u_1}}, p_2\widetilde{\widetilde{u_2}})dt < \int_0^\tau x_1(t; p_1\widetilde{u_1}, p_2\widetilde{u_2})dt,$$
$$\int_0^\tau x_2(t; p_1\widetilde{\widetilde{u_1}}, p_2\widetilde{\widetilde{u_2}})dt > \int_0^\tau x_2(t; p_1\widetilde{u_1}, p_2\widetilde{u_2})dt,$$

hold in the first case and the reverse inequalities hold in the second one. On the other hand, by the assumptions in **iv)**, system (4.8) has a unique solution in $\mathrm{Int}\mathbb{R}^2_+$ and so

$$\int_0^\tau x_1(t; p_1\widetilde{\widetilde{u_1}}, p_2\widetilde{\widetilde{u_2}})dt = \int_0^\tau x_1(t; p_1\widetilde{u_1}, p_2\widetilde{u_2})dt,$$
$$\int_0^\tau x_2(t; p_1\widetilde{\widetilde{u_1}}, p_2\widetilde{\widetilde{u_2}})dt = \int_0^\tau x_2(t; p_1\widetilde{u_1}, p_2\widetilde{u_2})dt.$$

Thus we arrived at a contradiction, proving the uniqueness of the fixed point. The proof of **iv)** follows from Theorem 3.1, considering the set $D = (0, u_1^* + \varepsilon) \times (0, u_2^* + \varepsilon)$ given in Proposition 3.3. □

In the absence of inter- and intra-specific competition in (2.6), i.e., by setting $b_{ij} = 0$ for all i, j, in (2.7), system (2.6) is uncoupled and its dynamical behaviour is given by the thresholds A_i introduced in (4.3). Specifically, if $A_i < 1$, then $\lim_{t\to\infty} u_i(t) = 0$, and if $A_i > 1$ then $u_i(t)$ is unbounded. Although the competition at immature stages has no effect in the first case, the dynamical picture of (2.6) is completely different and much richer when $A_i > 1$. Proposition 4.1 and Theorem 4.1 provide sharp sufficient conditions for dominance or global attraction to a coexistence state.

5. Dynamics of (2.6) via Lotka–Volterra systems

In this section we study system (2.6), (2.7) with birth rates defined by

$$b_i(u_1, u_2) = \frac{p_i u_i}{1 + u_1 + u_2}, \quad i = 1, 2, \tag{5.1}$$

with $p_i > 1$. This choice is motivated by the classical Beverton–Holt equation and the Leslie–Gower model; see, e.g., [3] and its references.

Take $B(u_1, u_2) = (b_1(u_1, u_2), b_2(u_1, u_2))$ and $H(u_1, u_2) = (\frac{u_1}{\mu_1}, \frac{u_2}{\mu_2})$. In Appendix A, we show that B is the Poincaré map at time 1 of a Lotka–Volterra system (A.1). Using this result, we can see $\Delta = H \circ P \circ B$ as the Poincaré map of the $(2 + \tau)$-periodic system

$$\begin{aligned} x_1' &= x_1(a_1(t) - b_{11}(t)x_1 - b_{12}(t)x_2), \\ x_2' &= x_2(a_2(t) - b_{21}(t)x_1 - b_{22}(t)x_2), \end{aligned} \tag{5.2}$$

where

$$a_i(t) = \begin{cases} \log(p_i) & \text{if} \quad 0 \le t < 1 \\ -c_i & \text{if} \quad 1 \le t < 1 + \tau \\ -\log(\mu_i) & \text{if} \quad 1 + \tau \le t < 2 + \tau \end{cases}$$

and

$$b_{ij}(t) = \begin{cases} \frac{\log(p_i)}{p_i - 1} & \text{if} \quad 0 \le t < 1 \\ b_{ij} & \text{if} \quad 1 \le t < 1 + \tau \\ 0 & \text{if} \quad 1 + \tau \le t < 2 + \tau. \end{cases}$$

Thus, we can write $\Delta(u_1, u_2) = (u_1 h_1(u_1, u_2), u_2 h_2(u_1, u_2))$, where

$$\begin{aligned} h_1(u_1, u_2) &= \exp\left(\int_0^{2+\tau} a_1(t) - b_{11}(t)x_1(t, u_1, u_2) - b_{12}(t)x_2(t, u_1, u_2)dt \right), \\ h_2(u_1, u_2) &= \exp\left(\int_0^{2+\tau} a_2(t) - b_{21}(t)x_1(t, u_1, u_2) - b_{22}(t)x_2(t, u_1, u_2)dt \right), \end{aligned} \tag{5.3}$$

and $(x_1(t, u_1, u_2), x_2(t, u_1, u_2))$ is the solution of (5.2) with initial condition (u_1, u_2). Note that Δ meets conditions **(S1)–(S3)** introduced in Section 3.2; see, e.g. [7].

The numbers

$$A_i := h_i(0, 0) = \frac{p_i e^{-c_i \tau}}{\mu_i}, \; i = 1, 2, \tag{5.4}$$

determine the existence of semi-trivial fixed points of Δ.

Our next proposition shows that non-existence of semi-trivial equilibria in one of the axes implies extinction of the corresponding species. Its proof is analogous to the proof of Proposition 4.1, so we omit it.

Proposition 5.1. *Consider system (2.6) with reproduction functions (5.1).*

1. *If $A_i \le 1$ for $i = 1, 2$ then $(0, 0)$ is a global attractor for (2.6).*
2. *If $A_1 > 1$ and $A_2 \le 1$ then there is $u_1^* > 0$ so that $(u_1^*, 0)$ is a global attractor for (2.6).*
3. *If $A_1 \le 1$ and $A_2 > 1$, then there is $u_2^* > 0$ so that $(0, u_2^*)$ is a global attractor for (2.6).*

The abstract setting of Section 3 allows us to infer dynamical properties of system (2.6) from the study of a planar map. We exploit this idea together with some powerful tools from planar dynamical systems such as the carrying simplex developed by Hirsch in [6] and some subtle properties on real analytic functions (see [16,18]). In this way, we deduce some interesting results that seem to be new even for planar competitive maps; for example, permanence implies the existence of an isolated coexistence state which is a local attractor.

Theorem 5.1. *Assume that $A_i > 1$ for $i = 1, 2$.*

i) *If*

$$\int_0^{2+\tau} a_1(t) - b_{12}(t)x_2(t; (0, u_2^*))dt > 0 \quad \text{and}$$

$$\int_0^{2+\tau} a_2(t) - b_{21}(t)x_1(t; (u_1^*, 0))dt > 0, \tag{5.5}$$

hold, then system (2.6) is permanent. Moreover, there is an isolated equilibrium in $\mathrm{Int}\mathbb{R}_+^2$ which is a local attractor.

ii) *If $\int_0^{2+\tau} a_1(t) - b_{12}(t)x_2(t; (0, u_2^*))dt < 0$ then $(0, u_2^*)$ is a local attractor for (2.6).*

iii) *If $\int_0^{2+\tau} a_2(t) - b_{21}(t)x_1(t; (u_1^*, 0))dt < 0$ then $(u_1^*, 0)$ is a local attractor for (2.6).*

Proof. Arguing as in the proof of Theorem 4.1, given any initial condition $(\phi_1(t), \phi_2(t))$ with $\phi_i(t) > 0$ for all $t \in [-\tau, 0]$, and $\varepsilon > 0$, there is $t_* = t_*(\varepsilon)$ so that

$$u_1(t, \phi(t)) \le u_1^* + \varepsilon, \quad u_2(t, \phi(t)) \le u_2^* + \varepsilon,$$

for all $t \ge t_*$.

Proof of i). Conditions (5.5) mean that $h_1(0, u_2^*) > 1$ and $h_2(u_1^*, 0) > 1$. In addition, we know that Δ is bounded and $h_1(0, 0) > 1$, $h_2(0, 0) > 1$. By Corollary 2.2 in [10] with Lyapunov functions $P(x, y) = x$ and $P(x, y) = y$, one can prove that system

$$\begin{aligned} x_{n+1} &= x_n h_1(x_n, y_n) \\ y_{n+1} &= y_n h_2(x_n, y_n) \end{aligned} \tag{5.6}$$

is permanent. The proof of the first part of **i)** follows from Theorem 3.2, considering the set $D = (0, u_1^* + \varepsilon) \times (0, u_2^* + \varepsilon)$ given in Remark 3.3 (we prove below that $\mathrm{Fix}(\Delta)$ is finite).

To prove the second claim in **i)**, we first note that, by Liouville's formula,

$$\det \Delta'(x, y) > 0, \quad \forall (x, y) \in \mathbb{R}_+^2.$$

Next, by Lemma 3.3, function Δ satisfies condition **(C2)** of Theorem 3.4, and therefore we only need to prove that Δ has an isolated local attractor in $\mathrm{Int}\mathbb{R}_+^2$.

First we prove that $\mathrm{Fix}(\Delta)$ is finite. By the proof of Theorem 3.4, there is a carrying simplex Γ satisfying **(CS1)–(CS3)**, which contains all nontrivial fixed points of Δ. On the other hand, $\Upsilon = \Delta - Id_2$ is a real analytic function (see [13] for a precise definition), and by **(S3)**, $\Upsilon'(p) \neq 0$ for all $p \in \mathrm{Int}\mathbb{R}_+^2$. Now, assume by contradiction that $Z = \{p : \Upsilon(p) = 0\}$ is not finite. As system (5.6) is permanent, Z has an accumulation point in $\mathrm{Int}\mathbb{R}_+^2$. By Lemma 1.2 in [18], the set Z' of accumulation points of Z is an open subset of Γ. Since Z' is closed in Γ and Γ is connected, it follows that $Z' = \Gamma$. This is a contradiction since (5.6) is permanent and $(u_1^*, 0)$, $(0, u_2^*)$ belong to Γ.

Now we prove that if (5.6) is permanent and the number of equilibria is finite, then there is a local attractor in $\mathrm{Int}\mathbb{R}_+^2$. Arguing as in the proof of Theorem 3.4, we get that the map $g = p \circ \Delta|_\Gamma \circ p^{-1} : [0, u_1^*] \longrightarrow [0, u_1^*]$, where $p(x, y) = x$, is a strictly increasing homeomorphism. As system (5.6) is permanent, we have that $g(x) > x$ for all $x \in (0, \varepsilon)$, and $g(x) < x$ for all $x \in (u_1^* - \varepsilon, u_1^*)$, for a suitable $\varepsilon > 0$. By these properties, since g has a finite number of fixed points, it follows that g has at least one local attractor, say $\widetilde{u_1}$. Therefore, $(\widetilde{u_1}, \widetilde{u_2})$, where $\widetilde{u_2}$ is the unique point satisfying $(\widetilde{u_1}, \widetilde{u_2}) \in \Gamma$, is an isolated local attractor for Δ.

Finally, by Theorem 3.4, $(\widetilde{u_1}, \widetilde{u_2})$ is a strong attractor for Δ, and the proof follows from Theorem 3.1.

Proof of ii) and iii). The proof is exactly the same as in Theorem 4.1 **iii)**, using that, by our assumptions, $h_1(0, u_2^*) < 1$ in case **ii)**, and $h_2(u_1^*, 0) < 1$ in case **iii)**. □

Remark 5.1. To verify the inequalities involved in statement **i)** of the previous theorem, it is worth noticing that the solutions of (5.2) with initial conditions $(u_1^*, 0)$ and $(0, u_2^*)$ satisfy, respectively, the following inequalities:

$$\max\{x_1(t; (u_1^*, 0)) : t \in [0, 2 + \tau)\} \leq p_1 \max\left\{1, \frac{1}{\mu_1}\right\},$$

$$\max\{x_2(t; (0, u_2^*)) : t \in [0, 2 + \tau)\} \leq p_2 \max\left\{1, \frac{1}{\mu_2}\right\}.$$

In the next results we establish sufficient conditions for global extinction of one of the species and for global attraction to a coexistence state in (2.6). The method of proof is inspired by the analysis of Lotka–Volterra systems (see, e.g., [22]).

Theorem 5.2. *Assume that $A_i > 1$ for $i = 1, 2$. If*

$$\frac{\log A_2}{\log A_1} < \min\left\{\frac{b_{21}}{b_{11}}, \frac{b_{22}}{b_{12}}, \frac{(p_1-1)\log p_2}{(p_2-1)\log p_1}\right\}, \tag{5.7}$$

then $(u_1^*, 0)$ is a global attractor for (2.6).

Proof. It is easy to check that condition (5.7) implies that there is $\kappa > 0$ such that

$$\frac{\int_0^{2+\tau} a_2(t)dt}{\int_0^{2+\tau} a_1(t)dt} < \kappa < \frac{b_{21}(t)}{b_{11}(t)}, \tag{5.8}$$

and

$$\frac{\int_0^{2+\tau} a_2(t)dt}{\int_0^{2+\tau} a_1(t)dt} < \kappa < \frac{b_{22}(t)}{b_{12}(t)} \tag{5.9}$$

hold for all $t \in [0, 1+\tau)$. First we prove that Δ has no fixed points in $\mathrm{Int}\mathbb{R}^2_+$. Indeed, take $(x_1(t), x_2(t))$ a solution of (5.2) in $\mathrm{Int}\mathbb{R}^2_+$, and consider

$$V(t) = x_1(t)^{-\kappa} x_2(t).$$

We claim that $V(0) \neq V(2+\tau)$. For $t \in [0, 2+\tau]\backslash\{1, 1+\tau\}$,

$$V'(t) = V(t)(a_2(t) - \kappa a_1(t) + x_1(t)(\kappa b_{11}(t) - b_{21}(t)) + x_2(t)(\kappa b_{12}(t) - b_{22}(t))).$$

Observe that, by (5.8)–(5.9),

$$\int_0^{2+\tau} a_2(t) - \kappa a_1(t) + x_1(t)(\kappa b_{11}(t) - b_{21}(t)) + x_2(t)(\kappa b_{12}(t) - b_{22}(t))dt < 0,$$

and so $\log V(2+\tau) - \log V(0) < 0$. This excludes the possibility of a $(2+\tau)$-periodic solution in (5.2). Now we prove that $h_1(0, u_2^*) > 1$. Indeed, as $h_2(0, u_2^*) = 1$, we get from (5.3) that

$$\int_0^{2+\tau} a_2(t)dt = \int_0^{2+\tau} b_{22}(t)x_2(t; (0, u_2^*))dt. \tag{5.10}$$

Hence, using (5.3), (5.9) and (5.10), we obtain

$$\begin{aligned} h_1(0, u_2^*) &= \exp\left(\int_0^{2+\tau} a_1(t) - b_{12}(t)x_2(t; (0, u_2^*))dt\right) \\ &> \exp\left(\int_0^{2+\tau} a_1(t) - \frac{1}{\kappa} b_{22}(t)x_2(t; (0, u_2^*))dt\right) \\ &= \exp\left(\int_0^{2+\tau} a_1(t) - \frac{1}{\kappa} a_2(t)dt\right), \end{aligned}$$

and therefore $h_1(0, u_2^*) > 1$ by (5.8).

Finally, the proof of Theorem 5.2 follows from Proposition 3.2 and Theorem 3.3, arguing as in the proof of statement **i)** of Theorem 4.1. □

Theorem 5.3. *Assume that $A_i > 1$ for $i = 1, 2$ and inequalities (5.5) hold. If*

$$\frac{b_{21}}{b_{11}} < \frac{(p_1 - 1)\log p_2}{(p_2 - 1)\log p_1} < \frac{b_{22}}{b_{12}}, \tag{5.11}$$

then there is an equilibrium of (2.6) in $\mathrm{Int}\mathbb{R}_+^2$ which is a global attractor.

Proof. Existence of a fixed point in $\mathrm{Int}\mathbb{R}_+^2$ follows arguing as in the proof of Theorem 4.1.

We claim that Δ has a unique fixed point in $\mathrm{Int}\mathbb{R}_+^2$. Assume, by contradiction, that there are two fixed points $(\widetilde{u}_1, \widetilde{u}_2)$, $(\widetilde{\widetilde{u}}_1, \widetilde{\widetilde{u}}_2)$; following again an argument from the proof of Theorem 4.1, we can assume that $\widetilde{u}_1 > \widetilde{\widetilde{u}}_1$ and $\widetilde{u}_2 < \widetilde{\widetilde{u}}_2$. Denote

$$\kappa := \frac{(p_1 - 1)\log p_2}{(p_2 - 1)\log p_1},$$

so that (5.11) becomes

$$\frac{b_{21}}{b_{11}} < \kappa < \frac{b_{22}}{b_{12}},$$

and define

$$V(t) = \kappa(X_1(t) - Y_1(t)) + (Y_2(t) - X_2(t)),$$

where $X_i(t) = \log x_i(t; (\widetilde{u}_1, \widetilde{u}_2))$ and $Y_i(t) = \log x_i(t; \widetilde{\widetilde{u}}_1, \widetilde{\widetilde{u}}_2)$, $i = 1, 2$. Since (5.2) preserves the order induced by the fourth quadrant, we get

$$X_1(t) > Y_1(t), \quad X_2(t) < Y_2(t),$$

for all $t > 0$. Next, since

$$\begin{aligned} V'(t) = &-(\kappa b_{11}(t) - b_{21}(t))(x_1(t, \widetilde{u}_1, \widetilde{u}_2) - x_1(t, \widetilde{\widetilde{u}}_1, \widetilde{\widetilde{u}}_2)) \\ &- (b_{22}(t) - \kappa b_{12}(t))(x_2(t, \widetilde{\widetilde{u}}_1, \widetilde{\widetilde{u}}_2) - x_2(t, \widetilde{u}_1, \widetilde{u}_2)), \end{aligned}$$

we get, using the definition of κ, that

$$V'(t) = \begin{cases} 0, & \text{if } t \in (0, 1) \\ -(\kappa b_{11} - b_{21})(e^{X_1(t)} - e^{Y_1(t)}) - (b_{22} - \kappa b_{12})(e^{Y_2(t)} - e^{X_2(t)}), & \text{if } t \in (1, 1+\tau) \\ 0, & \text{if } t \in (1+\tau, 2+\tau). \end{cases}$$

Thus, we have that

$$V(2+\tau) - V(0) = \int_0^{2+\tau} V'(t)dt < 0,$$

a contradiction that proves our claim. The rest of the proof follows employing the same arguments used in the proof of Theorem 4.1, that is, applying Propositions 3.1 and 3.3 together with Theorems 3.1 and 3.2. □

The previous results highlight the key role of inter and intra-specific competition during immature stages. To illustrate this fact, notice that if $b_{ij} = 0$ for all i, j, and

$$A_2 > A_1 > 1, \tag{5.12}$$

then the equilibrium $(0, A_2 - 1)$ is a global attractor for (2.6). Observe that in this case Δ is given by

$$\Delta(x_1, x_2) = \left(\frac{A_1 x}{1 + x + y}, \frac{A_2 y}{1 + x + y} \right),$$

and we can apply Proposition 3.2 and Theorem 3.3.

However, if b_{ij} are positive (so there is competition between immature individuals), Theorems 5.2 and 5.3 provide sufficient conditions to avoid the global dominance of the second species, leading to a coexistence state or giving dominance to the first species. In particular, by Theorem 5.2, we have global dominance of the first species if the following inequalities hold:

$$\frac{\log A_2}{\log A_1} < \frac{(p_1 - 1)\log p_2}{(p_2 - 1)\log p_1}, \tag{5.13}$$

$$\frac{\log A_2}{\log A_1} < \min\left\{ \frac{b_{21}}{b_{11}}, \frac{b_{22}}{b_{12}} \right\}. \tag{5.14}$$

Conditions (5.13)–(5.14) are compatible with (5.12). For a numerical example, take $p_1 = 5$, $p_2 = 15$, $a_2 = 2$, $a_1 = \tau = \mu_1 = \mu_2 = 1$, and any values of b_{ij} satisfying (5.14).

6. Ricker type birth rates

Motivated by the classical Ricker map and the related discrete system of two competing populations [15,20], we consider in this section the birth rate

$$B(u_1,u_2) := (B_1(u_1,u_2), B_2(u_1,u_2)) = (u_1 e^{r_1-u_1-a_{12}u_2}, u_2 e^{r_2-a_{21}u_1-u_2}), \tag{6.1}$$

with $0 < r_i < 1$, $a_{ij} > 0$, $i, j = 1, 2$. As in the previous section, we define $\Delta = H \circ P \circ B$. Recall that P is the Poincaré map of (2.7) and $H(u_1,u_2) = (\frac{u_1}{\mu_1}, \frac{u_2}{\mu_2})$. Direct calculations show that

$$\Delta(u_1,u_2) = (u_1 h_1(u_1,u_2), u_2 h_2(u_1,u_2)) \tag{6.2}$$

with

$$\begin{aligned} &h_1(u_1,u_2)\\ &= \frac{1}{\mu_1}\exp\left(r_1 - u_1 - a_{12}u_2 - c_1\tau - b_{11}\int_0^\tau x_1(t; B(u_1,u_2))dt - b_{12}\int_0^\tau x_2(t, B(u_1,u_2))dt\right),\\ &h_2(u_1,u_2)\\ &= \frac{1}{\mu_2}\exp\left(r_2 - u_2 - a_{21}u_1 - c_2\tau - b_{21}\int_0^\tau x_1(t; B(u_1,u_2))dt - b_{22}\int_0^\tau x_2(t, B(u_1,u_2))dt\right). \end{aligned}$$

By simple integration of the scalar equation

$$x_i' = -c_i x_i - b_{ii} x_i^2,$$

we get that, if the following condition holds:

$$\frac{c_i}{\mu_i\left(c_i e^{c_i\tau} + b_{ii}(e^{c_i\tau} - 1)\right)} \le 1, \quad i = 1, 2, \tag{6.3}$$

then

$$H \circ P([0,1) \times [0,1)) \subset [0,1) \times [0,1).$$

It is easy to check that B satisfies properties **(S1)–(S3)** of Section 3.2 for $\alpha = \beta = 1$ (see [20]).

Hence, since $H \circ P$ satisfies **(S2)–(S3)**, it follows from Lemma 3.2 that, under condition (6.3), Δ fulfills properties **(S1)–(S3)** with $\alpha = \beta = 1$.

Now we are in a position to argue as in Section 5 to get similar results for system (2.6) with birth function (6.1). In this case, the threshold numbers that determine the existence of semi-trivial equilibria are

$$A_i := h_i(0,0) = \frac{1}{\mu_i} e^{r_i - c_i \tau}, \quad i = 1, 2.$$

Thus, we have the following analogous result to Proposition 5.1:

Proposition 6.1. *Consider system (2.6) with birth function (6.1), and assume that (6.3) holds.*

1. *If $A_i \leq 1$ for $i = 1, 2$ then $(0,0)$ is a global attractor for (2.6).*
2. *If $A_1 > 1$ and $A_2 \leq 1$ then there is $u_1^* > 0$ so that $(u_1^*, 0)$ is a global attractor for (2.6).*
3. *If $A_1 \leq 1$ and $A_2 > 1$, then there is $u_2^* > 0$ so that $(0, u_2^*)$ is a global attractor for (2.6).*

In the same way, we can formulate a result of permanence similar to Theorem 5.1. To ensure permanence, we need to impose that $A_i > 1$ for $i = 1, 2$, and

$$h_1(0, u_2^*) > 1 \quad \text{and} \quad h_2(u_1^*, 0) > 1. \tag{6.4}$$

Under assumption (6.3), we easily have the following conditions implying (6.4):

$$r_1 - \log(\mu_1) - a_{12} - c_1\tau - b_{12}\tau > 0 \Longrightarrow h_1(0, u_2^*) > 1,$$
$$r_2 - \log(\mu_2) - a_{21} - c_2\tau - b_{21}\tau > 0 \Longrightarrow h_2(u_1^*, 0) > 1.$$

In the following results, we establish sufficient conditions to ensure global attraction to a semi-trivial equilibrium or to a coexistence equilibrium in the line of Theorems 5.2 and 5.3.

Theorem 6.1. *Consider system (2.6) with birth function (6.1), and assume that (6.3) holds and $A_i > 1$ for $i = 1, 2$. If*

$$\frac{r_2}{r_1} < \min\left\{\frac{\log \mu_2}{\log \mu_1}, \frac{c_2}{c_1}, \frac{b_{21}}{b_{11}}, \frac{b_{22}}{b_{12}}, a_{21}, \frac{1}{a_{12}}\right\},$$

then $(u_1^*, 0)$ is a global attractor.

Proof. Take $\kappa > 0$ so that

$$\frac{r_2}{r_1} < \kappa < \min\left\{\frac{\log \mu_2}{\log \mu_1}, \frac{c_2}{c_1}, \frac{b_{21}}{b_{11}}, \frac{b_{22}}{b_{12}}, a_{21}, \frac{1}{a_{12}}\right\}. \tag{6.5}$$

Here we look at Δ as the Poincaré map of the $(1+\tau)$-periodic system

$$\begin{aligned} x_1' &= x_1(a_1(t) - b_{11}(t)x_1 - b_{12}(t)x_2), \\ x_2' &= x_2(a_2(t) - b_{21}(t)x_1 - b_{22}(t)x_2), \end{aligned} \tag{6.6}$$

with initial condition $B(u_1, u_2)$, where

$$a_i(t) = \begin{cases} -c_i & \text{if} \quad 0 \le t < \tau, \\ -\log(\mu_i) & \text{if} \quad \tau \le t < 1+\tau, \end{cases}$$

and

$$b_{ij}(t) = \begin{cases} b_{ij} & \text{if} \quad 0 \le t < \tau, \\ 0 & \text{if} \quad \tau \le t < 1+\tau. \end{cases} \tag{6.7}$$

First we show that Δ has no fixed points in $\mathrm{Int}(\mathbb{R}^2_+)$. For it, given $(u_1, u_2) \in \mathrm{Int}\mathbb{R}^2_+$, we define

$$G(t) = x_1(t; B(u_1, u_2))^{-\kappa} x_2(t; B(u_1, u_2)),$$

where $(x_1(t; B(u_1, u_2)), x_2(t; B(u_1, u_2)))$ is the solution of (6.6) with initial condition $B(u_1, u_2)$. Notice that if (u_1, u_2) is a fixed point of Δ then $G(1+\tau) = u_1^{-\kappa} u_2$. To get a contradiction, we show that $G(1+\tau) < u_1^{-\kappa} u_2$. We split the proof into two steps: $G(0) < u_1^{-\kappa} u_2$ and $G(1+\tau) < G(0)$.

First, note that

$$G(0) = \frac{B_2(u_1, u_2)}{B_1(u_1, u_2)^\kappa} = u_1^{-\kappa} u_2 \exp\left((r_2 - \kappa r_1) - u_1(a_{21} - \kappa) - u_2(1 - \kappa a_{12})\right) < u_1^{-\kappa} u_2,$$

where in the last inequality we use (6.5).

On the other hand, for each solution $(x_1(t), x_2(t))$ of (6.6) in $\mathrm{Int}\mathbb{R}^2_+$, the function $\widetilde{G}(t) = x_1^{-\kappa}(t) x_2(t)$ satisfies that

$$\widetilde{G}'(t) = \widetilde{G}(t)((a_2(t) - \kappa a_1(t)) - x_1(t)(b_{21}(t) - \kappa b_{11}(t)) - x_2(t)(b_{22}(t) - \kappa b_{12}(t))).$$

Therefore, by (6.5),

$$\begin{aligned} &\log G(1+\tau) - \log G(0) \\ &= \int_0^{1+\tau} (a_2(t) - \kappa a_1(t)) - x_1(t)(b_{21}(t) - \kappa b_{11}(t)) - x_2(t)(b_{22}(t) - \kappa b_{12}(t)) dt < 0. \end{aligned}$$

Now we prove that $h_1(0, u_2^*) > 1$. Note that

$$h_1(0, u_2^*) = \frac{1}{\mu_1} \exp\left(r_1 - a_{12} u_2^* - c_1 \tau - b_{12} \int_0^\tau x_2(t, B(0, u_2^*)) dt \right), \tag{6.8}$$

and

$$h_2(0, u_2^*) = \frac{1}{\mu_2} \exp\left(r_2 - u_2^* - c_2 \tau - b_{22} \int_0^\tau x_2(t, B(0, u_2^*)) dt \right) = 1. \tag{6.9}$$

From (6.5), (6.8) and (6.9), we have:

$$\kappa \log h_1(0, u_2^*) = \kappa \left(-\log(\mu_1) + r_1 - a_{12}u_2^* - c_1\tau - b_{12} \int_0^\tau x_2(t, B(0, u_2^*))dt \right)$$
$$> -\log(\mu_2) + r_2 - u_2^* - c_2\tau - b_{22} \int_0^\tau x_2(t, B(0, u_2^*))dt$$
$$= -\log(\mu_2) + \log(\mu_2) = 0.$$

Finally, the proof of Theorem 6.1 is completed arguing as we did in the proof of Theorem 5.2. □

Theorem 6.2. *Consider system (2.6) with birth function (6.1), and assume that (6.3) holds, $A_i > 1$ for $i = 1, 2$, and inequalities (6.4) hold. If*

$$\max\left\{\frac{b_{21}}{b_{11}}, a_{21}\right\} < \min\left\{\frac{b_{22}}{b_{12}}, \frac{1}{a_{12}}\right\}, \tag{6.10}$$

then there is an equilibrium in $\mathrm{Int}\mathbb{R}^2_+$ *which is a global attractor for (2.6) in* $\mathrm{Int}\mathbb{R}^2_+$.

Proof. Since we follow the same arguments as in the proof of Theorem 5.3, we only need to prove that Δ cannot have more than one fixed point in $\mathrm{Int}\mathbb{R}^2_+$.

Assume by contradiction that there are two fixed points $(\widetilde{u}_1, \widetilde{u}_2)$, $(\widetilde{\widetilde{u}}_1, \widetilde{\widetilde{u}}_2)$. As in the proof of Theorem 5.3, it is not restrictive to assume that $\widetilde{u}_1 > \widetilde{\widetilde{u}}_1$ and $\widetilde{u}_2 < \widetilde{\widetilde{u}}_2$.

Now, as in the proof of Theorem 6.1, we look at Δ as the Poincaré map of the $(1 + \tau)$-periodic system (6.6) with initial condition $B(u_1, u_2)$.

By (6.10), we can choose a positive constant κ so that

$$\max\left\{\frac{b_{21}}{b_{11}}, a_{21}\right\} < \kappa < \min\left\{\frac{b_{22}}{b_{12}}, \frac{1}{a_{12}}\right\}. \tag{6.11}$$

Define

$$V(t) = \kappa(X_1(t) - Y_1(t)) + (Y_2(t) - X_2(t)),$$

where

$$X_i(t) = \log x_i(t; B(\widetilde{u}_1, \widetilde{u}_2)), \quad Y_i(t) = \log x_i(t; B(\widetilde{\widetilde{u}}_1, \widetilde{\widetilde{u}}_2)), \quad i = 1, 2,$$

and $(x_1(t; B(u_1, u_2)), x_2(t; B(u_1, u_2)))$ is the solution of (6.6) with initial condition $B(u_1, u_2)$.

As (6.6) preserves the order induced by the fourth quadrant, we have

$$X_1(t) > Y_1(t), \quad X_2(t) < Y_2(t),$$

for all $t > 0$. We aim to arrive at the contradiction

$$V(1 + \tau) < \kappa(\log \widetilde{u}_1 - \log \widetilde{\widetilde{u}}_1) + (\log \widetilde{\widetilde{u}}_2 - \log \widetilde{u}_2).$$

For it we check that $V(0) < \kappa(\log\widetilde{u}_1 - \log\widetilde{\widetilde{u}}_1) + (\log\widetilde{\widetilde{u}}_2 - \log\widetilde{u}_2)$ and $V(1+\tau) < V(0)$. Indeed, on the one hand we have that

$$\begin{aligned} V(0) &= \kappa(\log\widetilde{u}_1 - \log\widetilde{\widetilde{u}}_1) + (\log\widetilde{\widetilde{u}}_2 - \log\widetilde{u}_2) + (a_{21}-\kappa)(\widetilde{u}_1 - \widetilde{\widetilde{u}}_1) + (\kappa a_{12} - 1)(\widetilde{\widetilde{u}}_2 - \widetilde{u}_2) \\ &< \kappa(\log\widetilde{u}_1 - \log\widetilde{\widetilde{u}}_1) + (\log\widetilde{\widetilde{u}}_2 - \log\widetilde{u}_2). \end{aligned}$$

On the other hand, for all $t \in (0, 1+\tau)$,

$$\begin{aligned} V'(t) = &-(\kappa b_{11}(t) - b_{21}(t))(x_1(t, B(\widetilde{u}_1, \widetilde{u}_2)) - x_1(t, B(\widetilde{\widetilde{u}}_1, \widetilde{\widetilde{u}}_2))) \\ &- (b_{22}(t) - \kappa b_{12}(t))(x_2(t, B(\widetilde{\widetilde{u}}_1, \widetilde{\widetilde{u}}_2)) - x_2(t, B(\widetilde{u}_1, \widetilde{u}_2))). \end{aligned}$$

Thus, using (6.7) and (6.11), we get

$$V'(t) = \begin{cases} -(\kappa b_{11} - b_{21})(e^{X_1(t)} - e^{Y_1(t)}) - (b_{22} - \kappa b_{12})(e^{Y_2(t)} - e^{X_2(t)}) < 0, & \text{if } t \in (0, \tau), \\ 0, & \text{if } t \in (\tau, 1+\tau), \end{cases}$$

from where it follows that $V(1+\tau) - V(0) = \int_0^{1+\tau} V'(t)\,dt < 0.$ $\square$

Acknowledgments

This research has been supported by Ministerio de Economía y Competitividad (Spain), grant MTM2013-43404-P, a project co-funded by FEDER.

Appendix A

Consider the Lotka–Volterra system

$$\begin{aligned} x' &= x\left(\log p_1 - \frac{\log p_1}{p_1 - 1}x - \frac{\log p_2}{p_2 - 1}y\right), \\ y' &= y\left(\log p_2 - \frac{\log p_1}{p_1 - 1}x - \frac{\log p_2}{p_2 - 1}y\right), \end{aligned} \tag{A.1}$$

with $p_1, p_2 > 1$. We prove that the Poincaré map of (A.1) at time 1 is given by

$$B(x, y) = \left(\frac{p_1 x}{1 + x + y}, \frac{p_2 x}{1 + x + y}\right).$$

Indeed, using (A.1), we get

$$(x(t)/y(t))' = (x(t)/y(t))(\log p_1 - \log p_2).$$

After integration, we obtain

$$x(t;(x_0,y_0)) = y(t;(x_0,y_0))\frac{x_0}{y_0}\left(\frac{p_1}{p_2}\right)^t. \tag{A.2}$$

Replacing (A.2) into the second equation of (A.1), we get

$$y(1;(x_0,y_0)) = \frac{p_2 y_0}{1+x_0+y_0}. \tag{A.3}$$

Finally, from (A.2) and (A.3), it is clear that

$$x(1;(x_0,y_0)) = \frac{p_1 y_0}{1+x_0+y_0}.$$

References

[1] J.S. Armistead, J.R. Arias, N. Nishimura, L.P. Lounibos, Interspecific larval competition between *Aedes albopictus* and *Aedes japonicus* (Diptera: Culicidae) in northern Virginia, J. Med. Entomol. 45 (2008) 629–637.

[2] M.A.H. Braks, N.A. Honório, L.P. Lounibos, R. Lourenço-de-Oliveira, S.A. Juliano, Interspecific competition between two invasive species of container mosquitoes, *Aedes aegypti* and *Aedes albopictus* (Diptera: Culicidae), in Brazil, Ann. Entomol. Soc. Amer. 97 (2004) 130–139.

[3] J.M. Cushing, S. Levarge, N. Chitnis, S.M. Henson, Some discrete competition models and the competitive exclusion principle, J. Difference Equ. Appl. 10 (2004) 1139–1151.

[4] N.J. Gotelli, Competition and coexistence of larval ant lions, Ecology 78 (1997) 1761–1773.

[5] S. Gourley, R. Liu, Delay equation models for populations that experience competition at immature life stages, J. Differential Equations 259 (2015) 1757–1777.

[6] M.W. Hirsch, On existence and uniqueness of the carrying simplex for competitive dynamical systems, J. Biol. Dyn. 2 (2008) 169–179.

[7] M.W. Hirsch, H.L. Smith, Monotone dynamical systems, in: Handbook of Differential Equations: Ordinary Differential Equations, vol. II, Elsevier B.V., Amsterdam, 2005, pp. 239–357.

[8] S.B. Hsu, H.L. Smith, P. Waltman, Competitive exclusion and coexistence for competitive systems on ordered Banach spaces, Trans. Amer. Math. Soc. 348 (1996) 4083–4094.

[9] V. Hutson, The existence of an equilibrium for permanent systems, Rocky Mountain J. Math. 20 (1990) 1033–1040.

[10] V. Hutson, W. Moran, Persistence of species obeying difference equations, J. Math. Biol. 15 (1982) 203–213.

[11] J. Jiang, J. Mierczyński, Y. Wang, Smoothness of the carrying simplex for discrete-time competitive dynamical systems: a characterization of neat embedding, J. Differential Equations 246 (2009) 1623–1672.

[12] S. Juliano, L.P. Lounibos, Ecology of invasive mosquitoes: effects on resident species and on human health, Ecol. Lett. 8 (2005) 558–574.

[13] S.G. Krantz, H.R. Parks, A Primer of Real Analytic Functions, second ed., Birkhäuser Advanced Texts, Birkhäuser, Boston, MA, 2002.

[14] E. Liz, A. Ruiz-Herrera, Attractivity, multistability, and bifurcation in delayed Hopfield's model with non-monotonic feedback, J. Differential Equations 255 (2013) 4244–4266.

[15] R.M. May, G.F. Oster, Bifurcations and dynamic complexity in simple ecological models, Amer. Nat. 110 (1976) 573–599.

[16] F. Nakajima, G. Seifert, The number of periodic solutions of 2-dimensional periodic systems, J. Differential Equations 49 (1983) 430–440.

[17] G.F. O'meara, L.F. Evans, A.D. Gettman, J.P. Cuda, Spread of *Aedes albopictus* and decline of *Ae. aegypti* (Diptera: Culicidae) in Florida, J. Med. Entomol. 32 (1995) 554–562.

[18] R. Ortega, A. Tineo, On the number of positive periodic solutions for planar competing Lotka–Volterra systems, J. Math. Anal. Appl. 193 (1995) 975–978.

[19] A. Ruiz-Herrera, Exclusion and dominance in discrete population models via the carrying simplex, J. Difference Equ. Appl. 19 (2013) 96–113.

[20] H.L. Smith, Planar competitive and cooperative difference equations, J. Difference Equ. Appl. 3 (1998) 335–357.
[21] H.L. Smith, H.R. Thieme, Stable coexistence and bi-stability for competitive systems on ordered Banach spaces, J. Differential Equations 176 (2001) 195–222.
[22] A. Tineo, An iterative scheme for the n-competing species problem, J. Differential Equations 116 (1995) 1–15.