Simple dynamics in non-monotone Kolmogorov systems

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In this paper we analyse the global dynamical behaviour of some classical models in the plane. Informally speaking we prove that the folkloric criteria based on the relative positions of the nullclines for Lotka–Volterra systems are also valid in a wide class of discrete systems. The method of proof consists of dividing the plane into suitable positively invariant regions and applying the theory of translation arcs in a subtle manner. Our approach allows us to extend several results of the theory of monotone systems to nonmonotone systems. Applications in models with weak Allee effect, population models for pioneer-climax species, and predator–prey systems are given.

Keywords: Trivial dynamics; Geometric Criteria of global attraction; Nonmonotone systems; Planar systems

1. Introduction

The discrete equation

$$x_{n+1} = x_n g(x_n), \quad n \in \mathbb{Z}_+ = \{0, 1, 2, \ldots\}, \tag{1.1}$$

is a popular modeling framework for analysing the dynamical behaviour of a single species. In (1.1), $x_n \geqslant 0$ is the population density in the n-th generation and $g(x_n) \geqslant 0$ represents the density-dependent growth rate (or fitness function) from generation to generation. A common assumption in population dynamics is that g is decreasing. This means that the growth rate is mainly determined by negative density-dependent mechanisms such as intra-specific competition [5] or cannibalism. However, cooperative predation, resource defense, increased availability of mates and conspecific enhancement of reproduction are other biological mechanisms producing non-monotone growth rates, see [20]. For example, alders, big leaf maples,

poplars and some pine trees thrive at low densities and decrease at high ones due to overcrowding effects and other ecosystem constraints [**6**, **8**, **10**, **33**].

In describing the interactions of k species, a natural extension of equation (1.1) is

$$x_i(n+1) = x_i(n)H_i(x_1(n), \ldots, x_k(n)), \quad i = 1, \ldots, k. \tag{1.2}$$

The growth rate H_i is typically of the form

$$H_i(x_1(n), \ldots, x_k(n)) = g_i \left(\sum_{j=1}^{k} a_{ij}x_j(n) \right) \tag{1.3}$$

with $g_i : [0, +\infty) \longrightarrow [0, +\infty)$ a continuous function. In particular, if $a_{ij} > 0$ and g_i is decreasing for all $i, j = 1, \ldots, n$, system (1.2) describes the evolution of k competing species. See [**7**, **9**, **10**, **13**, **23**] and the references therein for a detailed discussion on these models.

Understading the dynamical behaviour of (1.2) is of critical importance from an applied point of view. There are several approaches for analysing this issue for competitive systems. For example, the convexity arguments given by Kon [**22**], the split Liapunov function method given by Baigent and Hou [**2**, **18**] or the theory of carrying simplex [**31**]. Recently, Hou [**16**, **17**] has provided a criterion of global attraction based on the relative position of the nullclines reminiscent to the classical results for the Lotka–Volterra system

$$\frac{dx_i}{dt} = x_i \left(r_i - \sum_{j=1}^{k} a_{ij}x_j \right), \quad i = 1, \ldots, k, \tag{1.4}$$

see [**1**] and the references therein. In contrast with the monotone case, the literature on non-monotone systems is relatively scarce. It is worth noting that system (1.2) can exhibit chaotic dynamics.

In this paper we describe the global dynamical picture of model (1.2) when the functions g_i are not necessarily decreasing. In particular, our criteria could be perceived as an extension of Hou's results to non-monotone systems. The method of proof is completely different from those papers mentioned above. First, we divide the phase space in suitable positively invariant regions and then we apply the theory of translation arcs [**3**, **12**, **27**] in a subtle manner. As emphasized in § 3, our conclusions are rather sharp.

The organization of the paper is as follows. In § 2, we introduce some notation and definitions. In § 3, we give the main results of the paper. Applications to population models for pioneer-climax species [**7**, **9**, **10**] and species with weak Allee effects [**20**] are discussed. To show the versatility of our results with different interactions, we discuss the dynamical behaviour of several classical predator–prey systems. We conclude the paper with a discussion on our findings.

2. Mathematical framework

The Euclidean disk with centre at $p = (p_1, p_2) \in \mathbb{R}^2$ and radius $R > 0$ is denoted by

$$D(p, R) = \{(x, y) \in \mathbb{R}^2 : \|(x, y) - (p_1, p_2)\| \leqslant R\}$$

with $\|(x, y)\| = \sqrt{x^2 + y^2}$. A subset of the plane homeomorphic to a (closed) Euclidean disk is called a topological disk. A map $h : V \subset \mathbb{R}^2 \longrightarrow V$ which is continuous and injective is called an embedding. Notice that if $h(V) = V$, then h is a homeomorphism. In this section, we work, without further mention, with embeddings defined on topological disks. We recall that $h : D \longrightarrow D$ is an orientation preserving embedding if it has degree one, that is,

$$\deg(h - q_0, U) = 1$$

where $h(p_0) = q_0$ with $p_0 \in Int D$ and $U \subset D$ is any open neighbourhood of p_0. The reader can consult the appendix in [27] for a detailed discussion on topological degree and index. When $h : D \longrightarrow D$ is an embedding of class $\mathcal{C}^1$, the sign of the determinant of the Jacobian matrix of h can determine whether h preserves the orientation. Specifically, if

$$\det Dh(x) > 0 \tag{2.1}$$

for all $x \in D$, then h is an orientation preserving embedding. Now we give a practical criterion to deduce when a map is an orientation preserving embedding. We have employed the notation ∂D to refer to the boundary of D in $\mathbb{R}^2$.

PROPOSITION 2.1. *Let $h : D \longrightarrow D$ be a map of class $\mathcal{C}^1$ with $D \subset \mathbb{R}^2$ a topological disk. Assume the following conditions:*

(i) $h(\partial D) \subset D$.

(ii) $\det Dh(x) > 0$ *for all $x \in D$.*

(iii) *There is a point $q \in D$ with a unique pre-image, that is, $h^{-1}(\{q\}) = \{p\}$.*

Then, $h(D) \subset D$ and

$$h : D \longrightarrow D$$

is an orientation preserving embedding.

Proof. Using that $h^{-1}(\{q\}) = \{p\}$ and that h is locally injective (by (ii)), we deduce that

$$h : D \longrightarrow h(D)$$

is a homeomorphism (see lemma 2.3.4 in [4]). We know that $h(D)$ is a topological disk with boundary contained in the topological disk D. This implies that $h(D) \subset D$ (see lemma 6 in [27, p. 39]). Hence,

$$h : D \longrightarrow D$$

is an embedding. Notice that h is an orientation preserving embedding because

$$\det Dh(x) > 0$$

for all $x \in D$. □

Given $h : D \longrightarrow D$ an embedding, the ω-limit set of a point $p \in D$ is defined as

$$\omega(h, p) = \{q \in D : h^{\sigma(n)}(p) \longrightarrow q \; for \; some \; sequence \; \sigma(n) \longrightarrow +\infty\}.$$

We say that h has trivial dynamics if for all $x \in D$,

$$\omega(h, x) \subset Fix(h)$$

where $Fix(h)$ denotes the fixed point set of h. It is worth noting that if h is dissipative and $\omega(h, x) \subset Fix(h)$ for all $x \in D$, then $\omega(h, x)$ is a connected set (see proposition 2 in [**27**], p. 42]). In particular, if h has a finite number of fixed points, then for all $x \in D$, there is $q \in Fix(h)$ so that $\omega(h, x) = \{q\}$. We stress that an embedding $h : D \longrightarrow D$ defined on a topological disk is always dissipative.

Next we recall two results based on the theory of translation arcs.

THEOREM 2.2 (Corollary 2.1 in [**30**], [**3**]). *Let $h : D \longrightarrow D$ be an orientation preserving embedding defined on the topological disk D. If $Fix(h) \subset \partial D$, then h has trivial dynamics.*

THEOREM 2.3 (Theorem 2.1 in [**26**], [**27**]). *Let $h : D \longrightarrow D$ be an orientation preserving embedding defined on the topological disk D. If $Fix(h) \cap IntD = \{q\}$ with $index(h, q) = -1$ then h has trivial dynamics.*

In the previous theorem, $index(h, q)$ denotes the usual topological index of h at q. We mention that theorem 2.1 in [**26**] deals with homeomorphisms. However, the same proof works for embeddings.

3. Geometric criteria of trivial dynamics

In this section we consider the system

$$\begin{cases} x_{n+1} = x_n g_1(x_n + \alpha y_n) \\ y_{n+1} = y_n g_2(y_n + \beta x_n) \end{cases} \tag{3.1}$$

with $\alpha, \beta > 0$ and $g_i : [0, +\infty) \longrightarrow (0, +\infty)$ a function of class $\mathcal{C}^1$ for $i = 1, 2$. Denote by

$$G(x, y) = (G_1(x, y), G_2(x, y)) = (xg_1(x + \alpha y), yg_2(y + \beta x)).$$

Notice that $G([0, +\infty)^2) \subset [0, +\infty)^2$. A common assumption for the single-species model (1.1), already stated by Ricker [**28**] and by Moran [**25**], is that there is a positive equilibrium p (the carrying capacity) so that

(C) $g(x) > 1$ for all $x \in (0, p)$ and $g(x) < 1$ for all $x > p$.

The previous condition can be adapted in model (3.1) as follows:

(P) For $i = 1, 2$, there exists $r_i > 0$ so that $g_i(x) > 1$ if $x \in (0, r_i)$ and $g_i(x) < 1$ if $x > r_i$.

Biologically, condition **(P)** means that the density of population of species i increases (resp. decreases) in the next generation when the weighted total biomass of both species is below (resp. above) a threshold.

In this section, we will make the assumption

(S) $\det DG(x, y) > 0$ for all $(x, y) \in \mathcal{R}$, where $\mathcal{R} = [0, A_1] \times [0, A_2]$ with

$$A_1 = \max\left\{r_1, \frac{r_2}{\beta}\right\}, \quad A_2 = \max\left\{r_2, \frac{r_1}{\alpha}\right\}.$$

Condition **(S)** implies that G is one-to-one on $\mathcal{R}$. The biological meaning of this is simple. If we take two different initial data, the densities of population are different each other in any future generation. To avoid technical problems, we also suppose:

(H) $g_i'(r_i) \neq 0$ for $i = 1, 2$.

Define

$$L_1 = \{(x, y) \in [0, +\infty)^2 : x + \alpha y = r_1\},$$
$$L_2 = \{(x, y) \in [0, +\infty)^2 : \beta x + y = r_2\},$$
$$\mathcal{L}_1^- = \{(x, y) \in [0, +\infty)^2 : x + \alpha y \leqslant r_1\}$$

and

$$\mathcal{L}_2^- = \{(x, y) \in [0, +\infty)^2 : \beta x + y \leqslant r_2\}.$$

The system has, at most, four equilibria namely $(0, 0)$, $(r_1, 0)$, $(0, r_2)$ and

$$(x^*, y^*) = \left(\frac{r_1 - \alpha r_2}{1 - \alpha\beta}, \frac{r_2 - \beta r_1}{1 - \alpha\beta}\right). \tag{3.2}$$

Obviously, the last equilibrium is located at the intersection of L_1 and L_2. In our analysis, we exclude the case $L_1 = L_2$ ($\alpha = \beta = 1$ and $r_1 = r_2$).

We prove that the relative position of L_1 and L_2 completely determines the dynamical behaviour of (3.1). This is a well-known result when the system is monotone. Our contribution will be to show that it is also true for non-monotone systems. We stress that if $(x, y) \in (0, +\infty)^2 \backslash \mathcal{R}$, then

$$\begin{cases} x > G_1(x, y) \\ y > G_2(x, y). \end{cases} \tag{3.3}$$

PROPOSITION 3.1. *Assume that* **(P)** *and* **(S)** *are satisfied. Then, $G(\mathcal{R}) \subset \mathcal{R}$ and*

$$G|_{\mathcal{R}} : \mathcal{R} \longrightarrow \mathcal{R}$$

is an orientation preserving embedding.

Proof. First we notice that $G^{-1}(\{0\}) = \{0\}$. Next we prove that $G(\partial\mathcal{R}) \subset \mathcal{R}$. Take a point of the form (A_1, y) with $y \in [0, A_2]$. We observe that $A_1 + \alpha y \geqslant r_1$ and $y + \beta A_1 \geqslant r_2$. Then, by condition **(P)**,

$$G_1(A_1, y) = A_1 g_1(A_1 + \alpha y) \leqslant A_1$$
$$G_2(A_1, y) = y g_2(\beta A_1 + y) \leqslant y \leqslant A_2.$$

Now, it is clear that

$$\{G(A_1, y) : y \in [0, A_2]\} \subset \mathcal{R}.$$

Analogously, we can prove that

$$\{G(x, A_2) : x \in [0, A_1]\} \subset \mathcal{R}.$$

We also observe that condition **(S)** ensures that $G_1(x, 0) = x g_1(x)$ and $G_2(0, y) = y g_2(y)$ are strictly increasing (they are locally injective and have two fixed points). Thus, $G([0, A_1] \times \{0\}) \subset [0, A_1] \times \{0\}$ and $G(\{0\} \times [0, A_2]) \subset \{0\} \times [0, A_2]$. Collecting the above information, we deduce that

$$G(\partial\mathcal{R}) \subset \mathcal{R}.$$

The conclusion now follows from proposition 2.1 immediately.   □

LEMMA 3.2. *Let* $\{(x_n, y_n)\}$ *be a sequence of* (3.1) *with initial condition* $(x_0, y_0) \notin \mathcal{R}$. *Assume that* **(P)** *and* **(S)** *hold. Then, one of the following properties is satisfied:*

  (i) $\{(x_n, y_n)\} \longrightarrow q$ *with* q *an equilibrium of* (3.1).

  (ii) *There exists* $n_0 \in \mathbb{N}$ *so that* $(x_n, y_n) \in \mathcal{R}$ *for all* $n \geqslant n_0$.

Proof. Assume that $(x_0, y_0) \in (0, +\infty)^2$. If $(x_n, y_n) \notin \mathcal{R}$ for all $n \in \mathbb{N}$, condition **(P)** ensures that $\{x_n\}$ and $\{y_n\}$ are strictly decreasing, see (3.3). Then, (i) holds. If there is $n_0 \in \mathbb{N}$ so that $(x_{n_0}, y_{n_0}) \in \mathcal{R}$, we deduce that $(x_n, y_n) \in \mathcal{R}$ for all $n \geqslant n_0$. Notice that $G(\mathcal{R}) \subset \mathcal{R}$ by the previous proposition. The case $x_0 = 0$ (resp. $y_0 = 0$) is treated in an analogous manner. Observe that in such a case $x_n = 0$ (resp. $y_n = 0$) for all $n \in \mathbb{N}$ and y_n (resp. x_n) is decreasing provided $y_n > A_2$ (resp. $x_n > A_1$).   □

REMARK 3.3. Lemma 3.2 says that it is enough for analysing the dynamical behaviour of (3.1) in $\mathcal{R}$. We repeatedly use this fact in the subsequent results.

The following result describes the behaviour of (3.1) on the axes.

LEMMA 3.4. *Assume that* **(P)** *and* **(S)** *hold. Then,* r_1 *and* r_2 *are globally asymptotically stable for*

$$x_{n+1} = x_n g_1(x_n)$$

and

$$y_{n+1} = y_n g_2(y_n)$$

respectively in $(0, +\infty)$.

Proof. We study the equilibrium r_1. The other case is analogous and we omit the details. By remark 3.3, we can restrict our attention on $[0, A_1]$. As mentioned in the proof of proposition 3.1, $\varphi(x) = x g_1(x)$ is strictly increasing in $[0, A_1]$. We remark that the unique fixed points of φ are 0 and r_1, and the fact $\varphi(A_1) \leqslant A_1$. By condition **(P)**, $g_1(x) > 1$ for all $x \in (0, r_1)$. Hence, $\varphi(x) > x$ for all $x \in (0, r_1)$. Now it is clear that 0 is unstable. Thus, r_1 is a global attractor for φ in $(0, A_1]$. $\square$

Now we are in a position to give the main result of this section.

THEOREM 3.5. *Assume* **(P)**, **(H)** *and* **(S)** *hold. Then the dynamical behaviour of* (3.1) *is as follows*:

   (i) $(r_1, 0)$ *is a global attractor in* $(0, +\infty)^2$ *provided* $\frac{r_2}{\beta} \leqslant r_1$ *and* $\frac{r_1}{\alpha} > r_2$.

   (ii) $(0, r_2)$ *is a global attractor in* $(0, +\infty)^2$ *provided* $\frac{r_2}{\beta} > r_1$ *and* $\frac{r_1}{\alpha} \leqslant r_2$.

   (iii) (x^*, y^*) *is a global attractor in* $(0, +\infty)^2$ *provided* $\frac{r_2}{\beta} > r_1$ *and* $\frac{r_1}{\alpha} > r_2$.

   (iv) *There is trivial dynamics in* (3.1) *with* $(r_1, 0)$ *and* $(0, r_2)$ *as local attractors in* $(0, +\infty)^2$ *provided* $\frac{r_2}{\beta} < r_1$ *and* $\frac{r_1}{\alpha} < r_2$.

Proof. First we realize that the origin is always a local repeller in $(0, +\infty)^2$. Indeed, by condition **(P)**, there is a neighbourhood U of the origin in $\mathcal{R}$ so that $g_1(x + \alpha y) > 1$ and $g_2(\beta x + y) > 1$ for all $(x, y) \in U$ with $x \neq 0$ and $y \neq 0$. This implies that $G_1(x, y) > x$ and $G_2(x, y) > y$ for all $(x, y) \in U$ with $x \neq 0$ and $y \neq 0$. Since $G((0, +\infty)^2) \subset (0, +\infty)^2$, it is clear that the origin is a local repeller in $(0, +\infty)^2$. We also stress that by remark 3.3, it is enough to study the dynamical behaviour in $\mathcal{R}$. Now we are ready to prove the theorem.

   (i) In this case, L_1 and L_2 do not intersect in $(0, +\infty)^2$. Then, $G|_{\mathcal{R}}$ has three fixed points, namely, $(0, 0)$, $(r_1, 0)$ and $(0, r_2)$. Since $Fix(G|_{\mathcal{R}}) \subset \partial\mathcal{R}$, theorem 2.2 and proposition 3.1 imply that for each $(x_0, y_0) \in Int\mathcal{R}$, there exists $q \in Fix(G|_{\mathcal{R}})$ so that

$$\omega(G|_{\mathcal{R}}, (x_0, y_0)) = \{q\}.$$

Next we prove that $q \neq (0, 0)$ and $q \neq (0, r_2)$. To see this, we check that both fixed points are local repellers in $(0, +\infty)^2$. At the beginning, we have already mentioned this fact for the origin. On the other hand, the eigenvalues of the linearized system at $(0, r_2)$ are

$$\{1 + r_2 g_2'(r_2), g_1(\alpha r_2)\} \tag{3.4}$$

where the associated eigenvectors are $(0, 1)$ and (w_1, w_2) with $w_1 \neq 0$ respectively. Since $r_1 > \alpha r_2$ and **(P)**, we conclude that $g_1(\alpha r_2) > 1$. On the other hand, we have already seen in the proof of proposition 3.1 that $\phi(y) = y g_2(y)$ is an increasing function. Moreover, $r_2 > 0$ is a global attractor of ϕ by lemma 3.4. Using these two facts together with **(H)**, we conclude that $\phi'(r_2) = 1 + r_2 g_2'(r_2) \in [0, 1)$. Observe that by **(S)**, $\phi'(r_2) \neq 0$. Now, it is clear that $(0, r_2)$ is a hyperbolic saddle point. In particular, it is a local repeller in $(0, +\infty)^2$.

   The proof of **(ii)** is analogous and we omit the details.

(iii) In this case, $G|_{\mathcal{R}}$ has four fixed points, namely, $(0, 0)$, $(r_1, 0)$, $(0, r_2)$ and (x^*, y^*). Define $\mathcal{A} = \mathcal{L}_1^- \cup \mathcal{L}_2^-$. The boundary of $\mathcal{A}$ is made of four segments: $\{0\} \times [0, \frac{r_1}{\alpha}]$, $[0, \frac{r_2}{\beta}] \times \{0\}$, l_1 and l_2 where l_1 is the segment on L_1 with ends at $(0, \frac{r_1}{\alpha})$ and (x^*, y^*) and l_2 is the segment on L_2 with ends at $(\frac{r_2}{\beta}, 0)$ and (x^*, y^*). Since $\frac{r_2}{\beta} > r_1$ and $\frac{r_1}{\alpha} > r_2$, we have that

$$l_1 \backslash \{(x^*, y^*)\} \subset [0, +\infty)^2 \backslash \mathcal{L}_2^- \tag{3.5}$$

and

$$l_2 \backslash \{(x^*, y^*)\} \subset [0, +\infty)^2 \backslash \mathcal{L}_1^-. \tag{3.6}$$

Then, given $(x, y) \in l_1$ different from the ends (x^*, y^*) and $(0, \frac{r_1}{\alpha})$, we have that $G_1(x, y) = x$ because $(x, y) \in l_1 \subset L_1$ and $G_2(x, y) < y$ by (3.5). Analogously,

$$G_1(x, y) < x$$
$$G_2(x, y) = y$$

for all $(x, y) \in l_2 \backslash \{(x^*, y^*), (\frac{r_2}{\beta}, 0)\}$. These expressions guarantee that

$$G|_{\mathcal{R}}(\partial \mathcal{A}) \subset \mathcal{A}.$$

Recall that the intervals $[0, A_1] \times \{0\}$ and $\{0\} \times [0, A_2]$ are positively invariant under G. Now, arguing as in the proof of proposition 2.1, we have that $G(\mathcal{A}) \subset \mathcal{A}$ and

$$G|_{\mathcal{A}} : \mathcal{A} \longrightarrow \mathcal{A}$$

is an orientation preserving embedding. A critical fact is that

$$Fix(G|_{\mathcal{A}}) \subset \partial \mathcal{A}.$$

Thus, if we apply theorem 2.2 to $G|_{\mathcal{A}}$, we conclude that for each $p \in \mathcal{A}$, there exists $q \in Fix(G|_{\mathcal{A}})$ so that

$$\omega(G|_{\mathcal{A}}, p) = \{q\}.$$

On the other hand, we notice that $\frac{r_2}{\beta} > r_1$, $\frac{r_1}{\alpha} > r_2$ and **(P)** imply that

$$g_2(\beta r_1) > 1 \text{ and } g_1(\alpha r_2) > 1.$$

Repeating the argument of the proof of **(i)**, we can prove $(r_1, 0)$ and $(0, r_2)$ are local saddle points. Recall that the origin is always a local repeller in $(0, +\infty)^2$. Consequently, for all $p \in \mathcal{A} \cap (0, +\infty)^2$,

$$\omega(G|_{\mathcal{A}}, p) = \{(x^*, y^*)\}.$$

Finally, we consider a sequence $\{(x_n, y_n)\}$ obtained from (3.1) so that $(x_0, y_0) \in \mathcal{R} \backslash \mathcal{A}$ with $x_0 > 0$ and $y_0 > 0$. By the same argument as that in lemma 3.2, one of the following facts holds:

h1 (x_n, y_n) tends to a fixed point of G.

h2 $(x_n, y_n) \in \mathcal{A}$ for all $n \geqslant n_0$ with n_0 large enough.
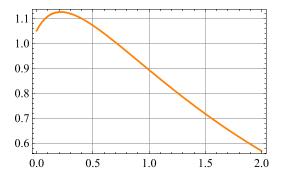
Figure 1. Representation of the function g in system (3.7) with $r = 0.5$, $a = 0.45$ and $b = 3$.

If **h1** holds, then the fixed point has to be (x^*, y^*) because the other fixed points are local repellers in $(0, +\infty)^2$. If **h2** holds, then we apply the above argument. The proof of **(iii)** is now completed.

(iv) In this case, $G|_{\mathcal{R}}$ has four fixed points, namely, $(0, 0)$, $(r_1, 0)$, $(0, r_2)$ and (x^*, y^*). By theorem 5.1 in [**32**], we deduce that

$$index(G, (x^*, y^*)) = -1.$$

Obviously, $index(G|_{\mathcal{R}}, (x^*, y^*)) = index(G, (x^*, y^*))$. Then, applying theorem 2.3 to $G|_{\mathcal{R}}$, we conclude that $G|_{\mathcal{R}}$ has trivial dynamics. Finally, linearizing the system and arguing as in **(i)**, we conclude that $(r_1, 0)$ and $(0, r_2)$ are local attractors. $\square$

EXAMPLE 3.6. Models with weak Allee effect.

The predation by a generalist predator with a saturating functional response is a common mechanism associated with the presence of weak Allee effects [**20**]. A natural extension in the plane of the single species models with this Allee effect is

$$\begin{cases} x_{n+1} = x_n g(x_n + \alpha y_n) \\ y_{n+1} = y_n g(y_n + \beta x_n), \end{cases} \quad (3.7)$$

where $\alpha, \beta > 0$,

$$g(x) = \exp\left(r(1 - x) - \frac{a}{1 + bx}\right)$$

with $r > a > 0$ and $b > 0$, see lemma 1.1 in [**20**].

Although g is not always monotone (see Fig. 1), we can apply theorem 3.5. Some particular choices of parameters are $r = 0.5$, $a = 0.45$ and $b = 3$ together with $\alpha = 0.5$ and $\beta = 0.6$ **(i)**; $\alpha = 1.1$ and $\beta = 0.6$ **(iii)**; $\alpha = 1.1$ and $\beta = 1.4$ **(iv)**. In general, condition **(S)** is difficult to verify in (3.7) because $\det DG(x, y)$ has a very complex expression. Notice that $detDG(x, y)$ can be negative for some points $(x, y) \in \mathcal{R}$ and for some choice of the parameters. Actually, system (3.7) can exhibit chaotic dynamics.

EXAMPLE 3.7. A nonmonotone version of May–Oster model [**24**].

Consider the system

$$
\begin{cases}
x_{n+1} = x_n g(x_n + \alpha y_n) \\
y_{n+1} = y_n g(y_n + \beta x_n),
\end{cases}
\tag{3.8}
$$

with $g(x) = \exp(x(r - x))$. After tedious computation, we can check that

$$
\det DG(x, y) > 0
$$

for all $(x, y) \in \mathcal{R}$ in the following range of parameters:

Case 1: $r = 0.1$, $\alpha \in (0.5, 1)$ and $\beta \in (3, 4.2)$.

Case 2: $r = 0.1$, $\alpha \in (0.5, 1)$ and $\beta \in (0.2, 0.5)$.

Case 3: $r = 0.1$, $\alpha \in (1, 6)$ and $\beta \in (1, 6)$.

As a direct application of theorem 3.5, we obtain that $(0.1, 0)$ is a global attractor in **case 1**, there is an interior fixed point (x^*, y^*) that is a global attractor in **case 2** and there is trivial dynamics with $(0.1, 0)$ and $(0, 0.1)$ as local attractors in **case 3**. As mentioned in the title of the example, (3.8) is a variant of the classical model discussed in [**24**]. We mention that this type of growth rates also appear in the evolution of climax species, see [**7**, **9**, **10**].

EXAMPLE 3.8. The conclusions in theorem 3.5 might not be true when the condition **(S)** does not hold.
Consider

$$
\begin{cases}
x_{n+1} = x_n g_1(x_n + \alpha y_n) \\
y_{n+1} = y_n g_2(y_n + \beta x_n)
\end{cases}
\tag{3.9}
$$

with $g_1(x) = \frac{r}{x+a}$ and $g_2(x) = \exp(p - qx)$, where $\alpha = \beta = a = 1$, $r = 21$, $p = 2.5$, $q = 0.1$. In this case, we have $\mathcal{R} = [0, 25] \times [0, 25]$. One can check that

$$
\det DG(0, 20) = -\sqrt{e} < 0,
$$

so condition **(S)** does not hold for model (3.9) because $(0, 20) \in \mathcal{R}$. As shown in [**7**], there is an asymptotically stable 2-cycle for this model so that the two species can coexist. This indicates that the conclusions in theorem 3.5 is not true for the model (3.9) by noticing that $\frac{r_2}{\beta} > r_1$ and $\frac{r_1}{\alpha} \leqslant r_2$.

4. Extinction in planar systems beyond (3.1)

Predator–prey models are prototypes of Kolmogorov systems in which the results of §3 are not directly applicable. However, some ideas developed in theorem 3.5 also work in these models. This shows the versatility of the mathematical framework given in §2.

Consider the system

$$\begin{cases} x_{n+1} = x_n f_1(x_n, y_n) \\ y_{n+1} = y_n f_2(x_n, y_n) \end{cases} \tag{4.1}$$

with f_1, $f_2 : [0, +\infty)^2 \longrightarrow (0, +\infty)$ functions of class $\mathcal{C}^1$. We denote by

$$F(x, y) = (F_1(x, y), F_2(x, y)) = (x f_1(x, y), y f_2(x, y))$$

the map associated with (4.1). To model the predator–prey iteraction, we assume the following conditions (x predator and y prey):

(PP1) $\frac{\partial F_1}{\partial x}(x, y) > 0$ and $\frac{\partial F_2}{\partial y}(x, y) > 0$ for all $(x, y) \in [0, +\infty)^2$.

(PP2) $\frac{\partial f_1(x, y)}{\partial y} > 0$ and $\frac{\partial f_1(x, y)}{\partial x} < 0$ for all $(x, y) \in [0, +\infty)^2$.

(PP3) $\frac{\partial f_2(x, y)}{\partial x} < 0$ and $\frac{\partial f_2(x, y)}{\partial y} < 0$ for all $(x, y) \in [0, +\infty)^2$.

(LG) There are two fixed points $(p^*, 0)$ and $(0, q^*)$ with p^*, $q^* > 0$ which are globally asymptotically stable on the x-axis and y-axis respectively.

(PP4) There is a constant $\widetilde{K} > 0$ so that $x f_1(x, q^* + 1) < x$ for all $x > \widetilde{K}$.

Condition (PP1) means that the intra-specific competition is contest (see [15]). (PP2) indicates that the growth rate of the predator is the result of the conjunction of two biological facts: the intra-specific competition and the consumption of the prey. (PP3) has an analogous meaning for the prey. (LG) says that each species in isolation has logistic growth rate with carrying capacities p^* and q^* respectively. (PP4) says that the predator density decreases in the next generation when it is above a suitable threshold.

We say that system (4.1) is permanent if there are two constants ε, $M > 0$ so that

$$\varepsilon \leqslant \liminf x_n \leqslant \limsup x_n \leqslant M$$

$$\varepsilon \leqslant \liminf y_n \leqslant \limsup y_n \leqslant M$$

for all sequence $\{(x_n, y_n)\}$ of (4.1) with initial condition $(x_0, y_0) \in (0, +\infty)^2$. Informally speaking, the notion of permanence excludes the extinction of some species in the system. To apply the classical theory of permanent systems we need to recall the notion of absorbing set. We say that a positively invariant set $\mathcal{R} \subset [0, +\infty)^2$ is an absorbing set for (4.1) if for all $(x_0, y_0) \in [0, +\infty)^2$, there is $n_0 \in \mathbb{N}$ so that $F^n(x_0, y_0) \in \mathcal{R}$ for all $n \geqslant n_0$.

The following lemma is an immediate consequence of lemma 2.1 in [19] by considering the average Liapunov function $V(x, y) = x^{\mu_1} y^{\mu_2}$. See also theorem 3.1 in [29].

LEMMA 4.1. *Assume that the map F associated with (4.1) has an absorbing set $\mathcal{R} := [0, K_1] \times [0, K_2]$ with $K_1, K_2 > 0$. If there are real numbers $\mu_1, \mu_2 > 0$ such*

that

$$\mu_1 \ln f_1(q) + \mu_2 \ln f_2(q) > 0 \tag{4.2}$$

for each q in $\Omega(\partial \mathcal{R}) := \bigcup_{p \in \partial \mathcal{R}} \omega(F, p)$, then (4.1) is permanent.

Next we give the main result of this section.

THEOREM 4.2. *Suppose that* **(PP1)**–**(PP4)** *and* **(LG)** *hold. Then every sequence of* (4.1) *is bounded. Moreover, we have the following conclusion:*

(i) *If $f_2(p^*, 0) > 1$, (4.1) is permanent.*

(ii) *If $f_2(p^*, 0) \leqslant 1$, $(p^*, 0)$ is a global attractor in $(0, +\infty)^2$.*

Proof. First, let us prove that $\mathcal{R} = [0, \widetilde{K}] \times [0, q^* + 1]$ is an absorbing set for (4.1). Take $\{(x_n, y_n)\}$ a sequence of (4.1). Define $\phi(y) = F_2(0, y)$. It follows from **(PP1)** and **(PP3)** that $\phi(y)$ is strictly increasing and $\phi(y) \geqslant F_2(x, y)$ for all $(x, y) \in [0, +\infty)^2$. From these properties we can deduce that

$$y_n \leqslant \phi^n(y_0) \tag{4.3}$$

for all $n \in \mathbb{N}$. Indeed,

$$y_1 = F_2(x_0, y_0) \leqslant \phi(y_0).$$

Repeating this argument, we obtain that

$$y_2 \leqslant \phi(y_1).$$

Using that ϕ is increasing and the previous step,

$$y_2 \leqslant \phi^2(y_0).$$

We complete the argument after a simple induction. Since $q^* > 0$ is a global attractor of

$$z_{n+1} = \phi(z_n)$$

in $(0, +\infty)$ by **(LG)** it is clear that there exists $n_1 \in \mathbb{N}$ so that $y_n \in [0, q^* + 1]$ for all $n \geqslant n_1$ by (4.3). Next we define $\varphi(x) = F_1(x, q^* + 1)$. By **(PP1)**, this function is strictly increasing. Using **(PP4)**, we have that for all $z_0 \in [0, +\infty)$, the sequence $\{z_n\}$ obtained from

$$z_{n+1} = F_1(z_n, q^* + 1)$$

satisfies that $z_n \longrightarrow q$ with $q < \widetilde{K}$. We also know by **(PP2)** that $F_1(x_n, y_n) \leqslant F_1(x_n, q^* + 1) = \varphi(x_n)$ for all $n \geqslant n_1$. Arguing as above, we can find $n_2 \geqslant n_1$ so that

$$x_n \in [0, \widetilde{K}]$$

for all $n \geqslant n_2$. Now, it is clear that $[0, \widetilde{K}] \times [0, q^* + 1]$ is an absorbing set for (4.1). Next we properly prove the theorem.

(i) It follows from **(LG)** that

$$\Omega(\partial\mathcal{R}) = \{(0,0), (p^*, 0), (0, q^*)\}.$$

Note that $f_1(p^*, 0) = 1$ and $f_2(0, q^*) = 1$ because $(p^*, 0)$ and $(0, q^*)$ are fixed points. Then, **(PP2)** and **(PP3)** imply that $f_i(0, 0) > 1$, $i = 1, 2$, and $f_1(0, q^*) > 1$. We know by assumptions that $f_2(p^*, 0) > 1$. At this moment, it is clear there are $\mu_1, \mu_2 > 0$ such that (4.2) holds for each $q \in \{(0, 0), (p^*, 0), (0, q^*)\}$. Hence (4.1) is permanent by lemma 4.1. **(ii)** It suffices to prove that every sequence of (4.1) with initial condition in $\mathcal{R}$ converges to $(p^*, 0)$. First we prove that (4.1) does not admit fixed points in $(0, +\infty)^2$. Assume, by contradiction, that $(p, q) \in (0, +\infty)^2$ is a fixed point of F. Then,

$$\begin{cases} 1 = f_1(p, q), \\ 1 = f_2(p, q). \end{cases} \tag{4.4}$$

By **(PP2)**, we obtain that

$$f_1(p^*, 0) = f_1(p, q) = 1 > f_1(p, 0).$$

Consequently, $p > p^*$. On the other hand, by **(PP3)**, we deduce that

$$1 = f_2(p, q) < f_2(p, 0) < f_2(p^*, 0) \leqslant 1,$$

a contradiction. After simple computations, we can prove that

$$\det DF(x, y) > 0$$

for all $(x, y) \in [0, +\infty)^2$. Moreover, it is clear that $F^{-1}(\{0\}) = \{0\}$. Then, by proposition 2.1, we have that

$$F|_{\mathcal{R}} : \mathcal{R} \longrightarrow \mathcal{R}$$

is an orientation preserving embedding. We notice that

$$Fix(F|_{\mathcal{R}}) \subset \partial\mathcal{R}.$$

Moreover, $f_1(0, 0) > 1$, $f_2(0, 0) > 1$ and $f_1(0, q^*) > 1$, (see the proof of **(i)**). Linearizing the system, we easily obtain that $(0, 0)$ is a local repeller. Regarding $(0, q^*)$, we have that $\{f_1(0, q^*), 1 + q^* \frac{\partial f_2}{\partial y}(0, q^*)\}$ are the eigenvalues of the linearized system. By **(PP1)** and **(PP3)**, $0 < \frac{\partial F_2}{\partial y}(0, q^*) = 1 + q^* \frac{\partial f_2}{\partial y}(0, q^*) < 1$. In other words, $(0, q^*)$ is a saddle point so that the repelling direction is (w_1, w_2) with $w_1 > 0$. The conclusion follows from theorem 2.2. $\qquad\square$

There are many classical models that satisfy conditions **(PP1)**–**(PP4)** and **(LG)**. For example,

$$\begin{cases} x_{n+1} = \dfrac{rx_n}{1 + x_n + h_1(y_n)} \\ y_{n+1} = \dfrac{sy_n}{1 + y_n + h_2(x_n)} \end{cases} \tag{4.5}$$

where $r > 1 + h_1(0)$, $s > 1 + h_2(0)$ and the functions $h_1, h_2 : [0, +\infty) \longrightarrow (0, +\infty)$ are of class $\mathcal{C}^1$ with $h_1'(x) < 0$ and $h_2'(x) > 0$ for all $x \in (0, +\infty)$.

5. Discussion

It is well known that the relative position of the nullclines determines the dynamical behaviour of the classical Lotka–Volterra model

$$\begin{cases} x' = x(r_1 - x - \alpha y) \\ y' = y(r_2 - y - \beta x). \end{cases} \tag{5.1}$$

In this paper we have proved that the same results remain true in a broad family of discrete systems, namely

$$\begin{cases} x_{n+1} = x_n g_1(x_n + \alpha y_n) \\ y_{n+1} = y_n g_2(y_n + \beta x_n). \end{cases} \tag{5.2}$$

In our analysis, we have imposed mainly the following:

(P) For $i = 1$, 2, there exists $r_i > 0$ so that $g_i(x) > 1$ if $x \in (0, r_i)$ and $g_i(x) < 1$ if $x > r_i$.

(S) $\det DG(x, y) > 0$ for all $(x, y) \in \mathcal{R}$ with $\mathcal{R} = [0, A_1] \times [0, A_2]$ with

$$A_1 = \max\left\{r_1, \frac{r_2}{\beta}\right\}, \quad A_2 = \max\left\{r_2, \frac{r_1}{\alpha}\right\}$$

and $G(x, y) = (xg_1(x + \alpha y), yg_2(y + \beta x))$.

The role of these conditions is critical. Notice that **(P)** is a necessary condition to maintain the dynamical behaviour of (5.1) in (5.2). On the other hand, if we drop **(S)**, as discussed in § 3, new phenomena emerge in (5.2) in comparison with (5.1). For example, the presence of 2-cycles or chaotic dynamics. It is worth stressing that condition **(P)** encompasses functions that are not monotone. Particularly, we can describe the dynamical behaviour of species subject to Allee effects. Other marked examples are the population models for pioneer-climax species that appears when g_1 is decreasing and g_2 is one-humped, see [**14**, **21**, **33**, **34**]. For a long time, the dominant topic in these models was mainly the exclusion of the pioneer species, ignoring other dynamical patterns. In contrast with this point of view, theorem 3.5 describes all the possible dynamical patterns. In particular, we study the exclusion for the climax species, which has also been analysed recently by Gilbertson and Kot [**11**].

There are many models in population dynamics that are not of the form (5.2), i.e., the growth rates are not a scalar function composed by a linear combination of the densities of the species. Nevertheless, many results are valid when the map associated with the model satisfies condition **(S)**. This is the case of most predator–prey systems with a generalist predator. For these models, we have proved that the absence of coexistence states leads to the exclusion of the prey. A direct consequence of this is that the presence of any oscillatory behaviour in $(0, +\infty)^2$ implies the existence of a coexistence state.

Acknowledgments

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