Competitive exclusion and coexistence in an $n$-species Ricker model

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We analyse a discrete-time Ricker competition model with $n$ competing species and give sufficient conditions, which depend on the competition coefficients only, for one species to survive (not necessarily at an equilibrium) and to drive all the other species to extinction. Our results complement and extend similar existing results from the literature. For the model reduced to three species ($n = 3$), we also investigate various scenarios under which all species coexist, in the sense that each species is robustly uniformly persistent. We provide a few numerical simulations to illustrate that coexistence does not necessarily mean convergence to the interior equilibrium, and that the interior dynamics can be quite complex.

Keywords: population dynamics; Ricker competition model; competitive exclusion; persistence

1. Introduction

Modelling population dynamics using Ricker-type functions is a very common approach in mathematical biology, being introduced for the first time by Ricker [8]. It is suitable for situations when the growth rate of the population is assumed to increase with increasing population size up to a certain value (the carrying capacity of the environment), after which it is assumed to decrease, due to a crowding effect and to competition for resources among the members of the population. Another modelling alternative, also very common, is to use Beverton–Holt-type functions for population growth rate. Such models, when used to study competition (among different subpopulations, species, etc.), are usually known as Leslie–Gower-type models [6]. They usually lead to simpler global dynamics, for example, of Lotka–Volterra-type [2,3], hence they predict competitive exclusion as the main outcome. One feature that facilitates the mathematical analysis of planar Leslie–Gower-type models is that these models generate monotone dynamics, for which a solid theoretical framework has been developed [11]. For higher dimensions (structured) models with two competing species, an approach, also based on some monotonicity of the system, is offered in [5].
Luis et al. [7] consider the following two-species Ricker competition model:

\begin{align}
  x_{n+1} &= x_n e^{K - x_n - a y_n}, \\
  y_{n+1} &= y_n e^{L - b x_n - y_n},
\end{align}

where constants $K$, $L$, $a$, $b$ are positive. The paper is concerned only with the local dynamics (around equilibria) of the model, for which a thorough analysis for the local stability is carried over, with an emphasis on the non-hyperbolic cases, when one eigenvalue corresponding to an equilibrium point has modulus one (the cases when both eigenvalues have modulus one are not discussed). The authors follow up on this model in [1], where they show, under a couple of technical assumptions, that the interior equilibrium of Equation (1) is globally asymptotically stable in the interior of the first quadrant, whenever it is locally asymptotically stable. However, the assumption that $1 \leq K, L \leq 2$ is made, in order to ensure that the dynamics on each axis is known (i.e. all nonzero solutions starting on either the $x$, or the $y$ axis, converge to $K$, or to $L$, respectively).

Regarding competitive exclusion for the Ricker model (1), Smith shows in [11] that, when an interior equilibrium does not exist, and when both carrying capacities $L$ and $K$ are less than or equal to one, the species with the larger competition coefficient drives the other species to extinction. More exactly, $y_n \to 0$ as $n \to \infty$, when $aL/K < 1 < bK/L$, while $x_n \to 0$ as $n \to \infty$, when $bK/L < 1 < aL/K$. Similar analysis for higher dimension versions of Equation (1), either for global convergence to an interior equilibrium, or for competitive exclusion, is not known to us.

In this paper we show, under some conditions on the competition coefficients that are independent of the intrinsic grown rates of the species, that a Ricker model of the type (1), with an arbitrary finite number of species, and having only boundary equilibria that belong to the coordinate axes, obeys the principle of competitive exclusion: one species survives, while all the other species go extinct. Also, motivated by numerical simulations suggesting that coexistence of species does not necessarily take the form of global convergence to an interior equilibrium, we offer sufficient condition for (robust) uniform persistence of all species in both models with two and three competing species.

2. Main results

2.1. Competitive exclusion

We consider the following $n$ species Ricker model:

\begin{equation}
  x_i(t+1) = x_i(t) \exp r_i \left( 1 - \sum_{j=1}^{n} c_{ij} x_j(t) \right), \quad i = 1, \ldots, n.
\end{equation}

Here, the interspecific competition coefficients $c_{ij} \geq 0$ for all $i, j = 1, \ldots, n, i \neq j$, and the intraspecific competition coefficients $c_{ii} = 1$ for all $i = 1, \ldots, n$ (i.e. all intraspecific competition coefficients are scaled to one). We want to find conditions such that the competitive exclusion principle applies to this model. Especially, we are interested in the possibility that species $x_1$ drives all the other species to extinction, but its dynamics are not trivial (i.e. $x_1(t)$ does not converge to an equilibrium).

First we give a couple of lemmas that will be used in the proof of some results in this section. To this end, it is routine to show that the system (2) is point dissipative. Hence,
there exists a compact set $B$ that attracts all solutions. For example, $B$ could be taken to be $\{x \in \mathbb{R}_+^n \mid x_i \leq b_i, \ i = 1, \ldots, n\}$, where $b_i = \max\{x_i \exp r_i(1 - \sum_{j=1}^n c_{ij}x_j) \mid \sum_{j=1}^n c_{ij}x_j \leq 1\}$. Hence, all solutions get into an arbitrary neighbourhood of $B$ and then remain in there for all subsequential times. For this reason, we can assume that $B$ absorbs all solutions (in the sense that all solutions enter $B$ and remain in $B$ for all subsequential times) and that it is also positively invariant.

Our first lemma gives uniform persistence of the total population.

**Lemma 2.1** The total population in Equation (2) is uniformly persistent: there exists $\varepsilon > 0$ such that

$$\liminf_{t \to \infty} |x(t)| > \varepsilon$$

for every solution $x(t)$ of Equation (2) with $|x(0)| > 0$.

**Proof** The conclusion follows directly from Proposition A.1 and Theorem A.1 in the appendix, applied with $M = \{0\}$.

The norm $\| \cdot \|$ that appears in the above lemma, and that we will use hereafter, is considered to be the $L^1$ norm but, in fact, any other norm can be considered, as all norms on $\mathbb{R}^n$ are equivalent.

**Remark 2.2** The uniform persistence of the total population (as given in the above lemma), as well as all the persistence results given in Section 2.2 are, in fact, robust (the persistence is uniform with respect to small changes in parameters; see, for example, [4,9] for more details on this concept). This follows from Theorem 3.2 in [9], because the assumptions $(H1) - (H3)$, as well as condition (20) in [9] are satisfied with the choice of $B$ as above. For simplicity, we have formulated all persistence results in this paper in the form of uniform persistence.

Using this lemma, without loss of generality, we can assume hereafter that $0 \notin B$.

Before we state our competitive exclusion result in regard to model (2) we need another lemma, whose proof can be found in the appendix. Although, for our purposes, a weaker version of this lemma would suffice, we state it here in a more general form. The set-up and idea of proof follows [9,10]. Thus, consider a difference equation of the form

$$x(t + 1) = f(x(t), y(t)),$$

$$y(t + 1) = A(x(t), y(t))y(t),$$

where $x \in \mathbb{R}_+^n$, $y \in \mathbb{R}_+^n$, and $A(x, y)$ is a continuous matrix function. Let $M = B \cap \{(x, y) \in \mathbb{R}_+^n \times \mathbb{R}_+^n \mid y = 0\}$. If $(x(t), y(t))$ is the solution of Equation (4) that satisfies $(x(0), y(0)) = z$, let

$$P(t, z) = A((x(t - 1), y(t - 1))) \cdot A((x(t - 2), y(t - 2))) \cdots A((x(0), y(0)));$$

$$\lambda(z, \eta) := \liminf_{t \to \infty} \frac{1}{t} \ln |P(t, z)\eta|, \ \eta \in \mathbb{R}_+^n.$$
Similarly, in regard to Equation (2), we can define

$$P_i(t, x) = \exp \left( r_i \left( t - \sum_{j=1}^{n} c_{ij} \sum_{k=0}^{t-1} x(k, x) \right) \right),$$  \hfill (8)

where \(x(t, x)\) is a solution of Equation (2), and

$$\lambda_i(x) = \limsup_{t \to \infty} \frac{1}{t} \ln P_i(t, x)$$

$$= \limsup_{t \to \infty} \frac{1}{t} r_i \left( t - \sum_{j=1}^{n} c_{ij} \sum_{k=0}^{t-1} x_j(t, x) \right).$$  \hfill (9)

**Lemma 2.4** The following holds:

(i) \(x_i > 0 \Rightarrow \lambda_i(x) \leq 0\);

(ii) \(\lambda_i(x) < 0 \Rightarrow \lim_{t \to \infty} x_i(t, x) = 0\);

(iii) \(\limsup_{t \to \infty} x_i(t, x) > 0 \Rightarrow \lambda_i(x) = 0\).

Although the proof of Lemma 2.3 is very similar to the proof of Lemma 4.1 in [10], we give it here, for completeness, in the appendix. Lemma 2.4 is the discrete-time version of Proposition 2 in [4]. Its proof is analogous to the proof of Proposition 2 in [4], thus we omit it.

Now we state our main result of this paper, which provides conditions under which species represented by \(x_1\) wins the competition by driving all the other species to extinction.

**Theorem 2.5** Assume that, for all \(i = 2, \ldots, n\), we have \(c_{1j} < c_{ij}\), for all \(j = 1, \ldots, i\). Then, \(x_i(t) \to 0\) as \(t \to \infty\), for all \(i = 2, \ldots, n\), for any solution \((x_1(t), \ldots, x_n(t))\) of Equation (2) satisfying \(x_1(0) > 0\).

**Proof** Let \(\tilde{\lambda}_i(x) = \limsup_{t \to \infty} (1/t)(t - \sum_{j=1}^{n} c_{ij} \sum_{k=0}^{t-1} x_j(t, x))\) (so that \(\lambda_i(x) = r_i \tilde{\lambda}_i(x)\)).

Let \(x \in B\) with \(x_1 > 0\). We show first that \(x_n(t, x) \to 0\), as \(t \to \infty\). Thus, from Lemma 2.4, we have that \(\tilde{\lambda}_1(x) \leq 0\). If \(x_n = 0\), then obviously \(x_n(t, x) = 0\), for all \(t \geq 0\). Assume now that \(x_n > 0\). Then again, \(\tilde{\lambda}_n(x) \leq 0\). If \(\tilde{\lambda}_n(x) < 0\), then \(x_n(t, x) \to 0\) as \(t \to \infty\) (see Lemma 2.4). Assume now that \(\tilde{\lambda}_n(x) = 0\). Then, \(\tilde{\lambda}_n(x) = 0\). But \(\tilde{\lambda}_n(x) \leq \tilde{\lambda}_1(x)\). Hence, \(\tilde{\lambda}_1(x) \geq 0\), from which it follows that

$$\tilde{\lambda}_1(x) = \tilde{\lambda}_n(x) = 0.$$  \hfill (10)

Furthermore, we have that

$$\sum_{j=1}^{n} (c_{nj} - c_{1j}) \sum_{k=0}^{t-1} x_j(k, x) \geq \min_{j=1, \ldots, n} (c_{nj} - c_{1j}) \sum_{k=0}^{t-1} |x(k, x)| \geq m_n t \quad \forall t \geq 1,$$  \hfill (11)

where \(m_n = \min_{j=1, \ldots, n} (c_{nj} - c_{1j}) \min_{x \in B} |x| > 0\). From Equation (11), we obtain

$$\frac{1}{t} \left( t - \sum_{j=1}^{n} c_{nj} \sum_{k=0}^{t-1} x_j(k, x) \right) \leq \frac{1}{t} \left( t - \sum_{j=1}^{n} c_{1j} \sum_{k=0}^{t-1} x_j(k, x) \right) - m_n \quad \forall t \geq 1.$$  \hfill (12)

Taking ‘lim sup’ as \(t \to \infty\) in both sides of Equation (12) and using Equation (10), we arrive to a contradiction.
By repeating the arguments above with \( n \) replaced by \( i = n - 1, n - 2, \ldots, 2 \), respectively, on the limit sets \( \{ x \in \mathbb{R}_+^n \mid x_n = \cdots = x_{i+1} = 0 \} \), we obtain that \( \omega(x) \cap M_i := \{ x \in B \mid x_2 = \cdots = x_n = 0 \} \neq \emptyset \).

Next we show that \( M_1 \) is locally attracting, which will complete the proof. For this, according to Lemma 2.3, it suffices to show that

\[
\lim \inf_{t \to \infty} \frac{1}{t} \ln |P(t,x)\eta| < 0 \quad \forall \; x \in M_1, \quad \eta \in \{ v \in \mathbb{R}_+^{n-1} \mid |v| = 1 \},
\]

where \( P(t,x) \) is the diagonal matrix with \( P_i(t,x), \; i = 2, \ldots, n \) on the main diagonal. In fact, we will show that Equation (13) holds with ‘lim inf’ replaced by ‘lim sup’. Thus, let \( x \in M_1, \; \eta \in \{ v \in \mathbb{R}_+^{n-1} \mid |v| = 1 \} \). Using Lemma 8.46 in [12], we have that

\[
\lim \sup_{t \to \infty} \frac{1}{t} \ln |P(t,x)\eta| = \max_i \left\{ \lim \sup_{t \to \infty} \frac{1}{t} \ln |P(t,x)e_i| \mid \eta_i > 0 \right\} \leq \max_i \lim \inf_{t \to \infty} \frac{1}{t} \ln P_i(t,x),
\]

where \( e_i = (0, \ldots, 0, 1, 0, \ldots, 0)^T, \; i = 1, \ldots, n \).

Using Lemma 2.1, we have

\[
\lim \sup_{t \to \infty} \frac{1}{t} \ln P_1(t,x) = 0.
\]

From this it follows that, for any \( \delta > 0 \), there exists \( T = T(\delta) \geq 0 \) such that

\[
\sum_{k=0}^{t-1} x_1(k,x) \geq t - \delta t \quad \forall \; t \geq T.
\]

Hence, using that \( c_{i1} > 1 \) for all \( i = 2, \ldots, n \) and Equation (16), we have

\[
\lim \inf_{t \to \infty} \frac{1}{t} \ln P_i(t,x) = \lim \inf_{t \to \infty} \frac{1}{t} \ln r_i \left( t - c_{i1} \sum_{k=0}^{t-1} x_1(k,x) \right) \\
\leq \lim \inf_{t \to \infty} \frac{1}{t} \ln r_i (t - c_{i1}(t - t\delta)) \\
= r_i (1 - c_{i1} + c_{i1}\delta) \\
< 0
\]

for \( \delta \) sufficiently small.

We mention that, for the planar case \( (n = 2) \), the same result is obtained in [11], but under the additional assumption \( r_1, r_2 \leq 1 \). This additional assumption is made in order to ensure that the system is order preserving (see [11] for definitions and details).

**Remark 2.6** Since \( c_{ii} = 1 \), the hypothesis of Theorem 2.5 is equivalent to \( c_{i1} < 1 \) and \( c_{ij} < c_{ij} \), for all \( i = 2, \ldots, n \) and \( j = 1, \ldots, i - 1 \). This hypothesis also implies the nonexistence of coexistence equilibria for Equation (2) (i.e. nonexistence of equilibria having more than one coordinate positive). Regarding the question of possibility of coexistence of species in a Ricker model of the form (2) (or an equivalent form), Balreira et al. [1] prove, under a few additional (technical) assumptions, that when an interior equilibrium exists and it is asymptotically stable, then it is also globally asymptotically stable in \( \text{int}(\mathbb{R}_+^2) \), the interior of \( \mathbb{R}_+^2 \). This is not, however, the only possibility of coexistence of all \( n \) species (i.e. in the form of globally asymptotically stable interior equilibrium), as numerical simulations in Section 3 suggest.
2.2. Coexistence

In this section, we investigate the possibility of long-term survival of one or more species in model (2). As mentioned in the previous sections, this happens in the form of robust uniform persistence, although for simplicity we present them in here in the form of uniform persistence.

**Lemma 2.7** Assume that, for all \( i = 2, \ldots, n \), there holds \( c_{ij} < c_{ij} \) for all \( j = 2, \ldots, i \). Then, the \( x_1 \) subpopulation in Equation (2) is uniformly persistent: there exists \( \varepsilon > 0 \) such that

\[
\liminf_{t \to \infty} |x_1(t,x)| > \varepsilon
\]

for every solution \( x(t,x) \) of Equation (2) with \( x_1 > 0 \).

**Proof** As above, according to Proposition 1 and Theorem 2.3 in [10], it suffices to show that \( \lambda_1(x) > 0 \) for all \( x \in M_1 := B \cap \{ x \in \mathbb{R}_+^n \mid x_1 = 0 \} \). Thus, suppose that \( \lambda_1(x) \leq 0 \) for some \( x \in M_1 \). Then, there exists \( i \in \{ 2, \ldots, n \} \) such that \( x_i > 0 \) (see Lemma 2.1). Assume that \( i \) is maximum with this property. Then, \( \lambda_i(x) \leq 0 \). We claim that \( \lambda_i(x) < 0 \). If not, then \( \lambda_i(x) = 0 \) and, using that \( x_1(t,x) = 0 \) for all \( t \geq 0 \) (because \( x_1 \in M_1 \)), we obtain that

\[
0 = \limsup_{t \to \infty} \frac{1}{t} \left( t - \sum_{j=2}^{n} c_{ij} \sum_{k=0}^{t-1} x_j(t,x) \right) \leq \limsup_{t \to \infty} \frac{1}{t} \left( t - \sum_{j=2}^{n} c_{ij} \sum_{k=0}^{t-1} x_j(t,x) \right),
\]

which implies that \( \lambda_1(x) \geq 0 \). Hence, \( \lambda_i(x) = \lambda_1(x) = 0 \). This leads to a contradiction, as in the proof of Theorem 2.1. Thus the claim holds, hence \( x_i(t,x) \to 0 \) as \( t \to \infty \) (see Proposition 1 in [4]). From this, it follows that \( 0 \in \omega(x) \), but this is a contradiction, according to Lemma 2.1. This concludes our proof.  

Next we investigate the possibility of coexistence of all species in model (2) (with \( n = 2 \) and \( n = 3 \)). Then, in the next section, offer a numerical simulation which shows that, in such a situation, there are solutions in \( \text{int} (\mathbb{R}_+^2) \), respectively, in \( \text{int} (\mathbb{R}_+^3) \), that do not converge to an interior equilibrium.

First, we address this issue for the system with just two species:

\[
\begin{align*}
    x_1(t+1) &= x_1(t) \exp (r_1(1-x_1(t)-c_{12}x_2(t))), \\
    x_2(t+1) &= x_2(t) \exp (r_2(1-c_{21}x_1(t)-x_2(t))).
\end{align*}
\]

**Lemma 2.8** If \( c_{12} < 1 \) and \( c_{21} < 1 \), then

\[
\exists \varepsilon, \delta > 0 \text{ such that } \liminf_{t \to \infty} \min\{x_1(t), x_2(t)\} > \varepsilon
\]

for all solutions \( x(t) \) of Equation (19) with \( x(0) = x \in \text{int} (\mathbb{R}_+^2) \).

**Proof** Let \( X_i = \{ x \in \mathbb{R}_+^2 \mid x_i = 0 \} \). Then, \( \Omega(X_i) = \{0\} \cup M_i \), where \( 0 \notin M_i \) and \( M_i \) is compact and invariant (see, e.g. [10]).

If we show that \( \lambda_i(x) > 0 \) for all \( x \in \{0\} \cup M_i, i = 1, 2 \), then Proposition 1 and Theorem 2.3 in [10] imply that Equation (20) holds.
Obviously, $\lambda_i(0) = r_i > 0$. Now let $x \in M_i$. Then, Equation (9) is equivalent to

$$
\lambda_i(x) = \limsup_{t \to \infty} \left( 1 - \frac{1}{t} c_{ij} S_j(t, x) \right), \quad i \neq j,
$$

where

$$
S_j(t, x) = \sum_{k=0}^{t-1} x_j(k, x).
$$

On the other hand,

$$
x_j(t, x) = x_j \exp(r_j(t - S_j(t, x))).
$$

Solving Equation (23) for $S_j(t, x)$ and substituting into Equation (21), we obtain

$$
\lambda_i(x) = \limsup_{t \to \infty} \left( 1 - c_{ij} + \frac{1}{tr_j} \ln \frac{x_j(t, x)}{x_j} \right) = 1 - c_{ij} > 0.
$$

Now we consider the case with three species.

**Theorem 2.9** If any of the following set of conditions is satisfied

(i) $c_{13}, c_{23} < 1$ and

\[
\begin{align*}
1 - c_{12} &< 1 - c_{23} &< 1 - c_{13}, \\
1 - c_{12} &< 1 - c_{23} &< 1 - c_{23}c_{32}, \\
1 - c_{12} &< 1 - c_{13} &< 1 - c_{13}c_{31}, \\
1 - c_{12} &< 1 - c_{12}c_{21} &< 1 - c_{12}c_{21} > 0;
\end{align*}
\]

(ii) $c_{13} > 1$ and Equations (25), (26) and Equations (28);

(iii) $c_{13}, c_{23} < 1$, Equations (26), (27) and

\[
\begin{align*}
c_{12}, c_{31}, c_{32} &< 1, \quad c_{21} > 1;
\end{align*}
\]

(iv) $c_{13} > 1, c_{23} < 1$, Equations (26) and (29);

(v) $c_{13} < 1, c_{23} > 1$, Equations (27) and (29);

then Equation (2) is uniformly persistent with respect to the interior of $\mathbb{R}_+^3$:

$$
\exists \varepsilon > 0 \text{ such that } \liminf_{t \to \infty} \min_{i=1,2,3} \{x_i(t, x)\} > \varepsilon
$$

for all solutions $x(t, x)$ of Equation (2) with $x \in \text{int}(\mathbb{R}_+^3)$.

**Proof** We only give the proof here corresponding to (i), as the other cases can be treated analogously.
Let $X_3 := \{ x \in \mathbb{R}^3_+ \mid x_3 = 0 \}$. From Lemma 2.8, we have that

$$\Omega(X_3) = \{ 0 \} \cup M_{23} \cup M_{13} \cup M_3,$$

where $M_{23} \subset \text{int}\{ x \in X_3 \mid x_2 = 0 \}$, $M_{13} \subset \text{int}\{ x \in X_3 \mid x_1 = 0 \}$ and $M_3 \subset \text{int}(X_3 \setminus \{ 0 \})$ are compact sets.

If we show that $\lambda_3(x) > 0$ for all $x \in \Omega(X_3)$, then Proposition 1 and Theorem 2.3 in [10] imply that Equation (30) holds with $\min_{i=1,2,3} \{ x_i(t,x) \}$ replaced by $x_3(t,x)$. Now, for any $x \in X_3$,

$$\lambda_3(x) = \limsup_{t \to \infty} \frac{1}{t} \ln \left( \prod_{k=0}^{t-1} \exp(r_3(1 - c_{31}x_1(k,x) - c_{32}x_2(k,x))) \right)$$

$$= \limsup_{t \to \infty} \frac{1}{t} (c_{31}S_1(t,x) + c_{32}S_2(t,x)),$$

where

$$S_i(t,x) = \sum_{k=0}^{t-1} x_i(k,x), \quad i = 1, 2.$$

Obviously, $\lambda_3(0) = r_3 > 0$. Next, let $x \in M_3$. Then, by iterating Equation (19), we obtain

$$x_1(t,x) = x_1 \exp(r_1(t - S_1(t,x) - c_{12}S_2(t,x))),$$

$$x_2(t,x) = x_2 \exp(r_2(1 - c_{21}S_1(t,x) - S_2(t,x))).$$

Solving Equation (34) for $S_1(t,x)$ and $S_2(t,x)$, we obtain

$$S_i(t,x) = \frac{1 - c_{ij}}{1 - c_{ij}} \frac{1}{r_i(1 - c_{ij})} \ln \frac{x_i(t,x)}{x_i} + \frac{c_{ij}}{r_j(1 - c_{ij})} \ln \frac{x_j(t,x)}{x_i}; \quad i, j = 1, 2, \quad ij = 2.$$  

Substituting $S_i(t,x)$ in Equation (32) and using Equation (28), we obtain that $\lambda_3(x) > 0$.

Finally, let $x \in M_{23}$, $j \in \{1, 2\}$. Then, by an argument analogous to the one in the proof of Lemma 2.8, we obtain that $\lambda_3(x) = 1 - c_{3j} > 0$, by Equation (25).

Thus, there exist $\varepsilon_1 > 0$ such that Equation (30) holds with $\varepsilon_1$ and with $\min_{i=1,2,3} \{ x_i(t,x) \}$ replaced by $x_3(t,x)$.

Let $B_3 = B \cap \{ x \in \mathbb{R}^3_+ \mid x_3 \geq \varepsilon_1 \}$ and $X_2 = \{ x \in \mathbb{R}^3_+ \mid x_2 = 0 \}$. Then,

$$\Omega(X_2 \cap B_3) = M_{12} \cup M_2,$$

where $M_{12} \subset \text{int}\{ x \in X_2 \cap B_3 \mid x_1 = 0 \}$ and $M_2 \subset \text{int}(X_2 \cap B_3)$ are compact sets.

As above, it can be shown that $\lambda_2(x) > 0$ for all $x \in \Omega(X_2 \cap B_3)$ and again, from Proposition 1 and Theorem 2.3 in [10] we obtain that there exist $\varepsilon_2 > 0$ such that Equation (30) holds with $\varepsilon_2$ and with $\min_{i=1,2,3} \{ x_i(t,x) \}$ replaced by $\min_{i=2,3} \{ x_i(t,x) \}$.

Finally, $\lambda_1(x) > 0$ for all $x \in \Omega(X_1 \cap B_{32})$, where $B_{32} = B \cap \{ x \in \mathbb{R}^3_+ \mid x_2, x_3 \geq \varepsilon_2 \}$ and $X_1 = \{ x \in \mathbb{R}^3_+ \mid x_1 = 0 \}$, from which Equation (30) follows.

3. Numerical simulations

In this section, we present a couple of numerical simulations in order to illustrate that uniform persistence does not necessarily take place in the form of global convergence of the interior solutions to an interior equilibrium, and that, in fact, the dynamics of these solutions can be quite
complicated, as shown in Figure 1(a) and 1(b) for the system (2) with two and, respectively, three species.

The parameters corresponding to Figure 1(b) were chosen to satisfy the conditions in part (iv) of Theorem 2.2.

Note that, in both simulations shown here, the single species dynamics (given by solutions with initial conditions belonging to the coordinate axes) are not trivial (since the $r_i$'s are greater than two).

4. Conclusion

In this study, we have addressed two major aspects of competition, namely competitive exclusion and coexistence, in the context of a discrete-time Ricker-type model.

In Theorem 2.1, we have provided a sufficient condition for one of the species, which we have chosen (without loss of generality) to be species $x_1$, to drive all the other species to extinction. In particular, we have shown that this happens if, for every $i = 2, \ldots, n, c_{ij} < c_{ij}$ for all $j = 2, \ldots, i$, which means that every species $x_i$ ($i = 2, \ldots, n$) competes harder against any other species $x_k$,
$k = 2, \ldots, i$, (including itself) than against species $x_1$. As a consequence, since the total population is shown to be uniformly persistent, species $x_1$ wins the competition and gets to survive alone above a positive threshold independent of all nonzero initial conditions.

In order to be able to obtain explicit conditions for coexistence of all species, we have restricted our study to models with two, respectively, three species, and have obtained such conditions that lead to uniform persistence. For the model with two species, these conditions (Lemma 2.8) agree with the general tenet regarding Lotka–Volterra competition models, namely that coexistence is possible when interspecific competition is small. For the model with three species, the same interpretation seems to apply, but the conditions become more complicated (Theorem 2.9). We have also offered a couple of numerical simulations to illustrate that coexistence does not necessarily mean convergence of all interior solutions to an interior equilibrium point.

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Appendix

The following two results, reproduced here from [10], are in regard to the system (4) and its subsequent notation. If \( P = \{E_0, \ldots, E_{k-1}\} \subseteq M \) is a periodic orbit \((E_0 \to E_1 \to \cdots \to E_{k-1} \to E_0)\), let

\[
A_i(P) = \begin{cases} A(E_{i-1}) \cdot \cdots \cdot A(E_0)A(E_{k-1}) \cdot \cdots \cdot A(E_i), & \text{if } i > 0 \\ A(E_{k-1}) \cdot \cdots \cdot A(E_0), & \text{if } i = 0. \end{cases}
\]

The spectral radius of \( A_i(P) \) has the same value for each \( i = 0, \ldots, k-1 \) and denote this common value by \( r(P) \). Let

\[
\Omega(M) = \cup_{z \in M} \omega(z). \tag{A2}
\]

**Proposition A.1** Assume that \( \Omega(M) \) is a union of periodic orbits and the following hold:

(i) \( \forall P = \{E_0, \ldots, E_{k-1}\} \subseteq \Omega(M) \) a periodic orbit, \( \exists \) such that \( A_i(P) \) is primitive,

(ii) \( r(P) > 1 \), for each periodic orbit \( P \subseteq \Omega(M) \),

(iii) \( A(z) \eta \neq 0 \), \( \forall (z, \eta) \in M \times U_+ \).

Then \( M \) is a uniformly weak repeller.

**Theorem A.2** Assume \( M \) is either empty or a uniformly weak repeller. Then

\[
\exists \varepsilon > 0 \text{ such that } \liminf_{t \to \infty} |y(t)| > \varepsilon,
\]

for all solutions \((x(t), y(t))\) of Equation (4) with \(|y(0)| > 0\).

Below we give a proof of Lemma 2.3.

**Proof** First notice that both \( M \) and \( U \) are compact sets. Let \( W = M \times U \) (so \( W \) is also compact) and \( \hat{w} = (\hat{z}, \hat{y}) \in W \).

Since \( \lambda(\hat{z}, \hat{y}) < 0 \), we have that there exists \( \hat{N} = \hat{N}(\hat{z}, \hat{y}) \geq 1 \) such that \(|P(\hat{N}, \hat{z}, \hat{y})| < 1 \). The function \((z, \eta) \mapsto |P(\hat{N}, z, \eta)|\) being continuous, there exist \( \delta_w > 0 \), \( c_w < 1 \) such that

\[
|P(\hat{N}, z, \eta)| < c_w, \quad \forall w = (z, \eta) \in B_{\delta_w}(\hat{w}) := \{w \in \mathbb{R}^{p+q} \times U \mid |w - \hat{w}| < \delta_w\}. \tag{A3}
\]

Since \( W \) is compact, there exists a finite set \( \{w^1, \ldots, w^k\} \subseteq W \) such that \( W \subseteq C := \cup_{i=1}^k B_{\delta_{w^i}}(w^i) \), where for every \( i = 1, \ldots, k \), \( \delta_{w^i} \) is the quantity corresponding to \( w^i \), coming from (A3) (i.e., for every \( i = 1, \ldots, k \), (A3) is satisfied with \( w \) replaced by \( w^i \)). To simplify notation, let \( N_i := N(w^i) \), \( \delta_i := \delta_{w^i}, i = 1, \ldots, k \). Also, let \( c := \max c_{w^i} \) (hence \( c < 1 \)) and \( N = \max N_i \). Thus, from (A3) we have that

\[
|P(N_i, z_0)\eta| < c, \quad \forall w = (z_0, \eta) \in B_{\delta_i}(w^i), \quad \forall i = 1, \ldots, k. \tag{A4}
\]

There exists \( \varepsilon > 0 \) such that \( N_i := [x, y] \in B \mid |y| < \varepsilon \times U \subset C \).

Now let \( z_0 \in N_i \). If \( z_0 \in M \) there is nothing left to prove. Thus, assume \( z_0 \not\in M \) (so \( |y| > 0 \)). Then there exists \( i_1 \in \{1, \ldots, k\} \) such that \( z_0 \in B_{\delta_{w_i}}(w^i) \). Hence, from Equation (A4) we have that \(|P(N_{i_1}, z_0)\eta| < c\). This implies

\[
\frac{|P(N_{i_1}, z_0)\eta|}{|P(N_{i_1}, \eta)|} < c. \tag{A5}
\]

In particular, \((z(N_{i_1}, z_0), P(N_{i_1}, \eta))|y_0|/|P(N_{i_1}, z_0)| \in C \). So there exists \( i_2 \in \{1, \ldots, k\} \) such that

\[
\left| \frac{P(N_{i_2}, z(N_{i_1}, z_0))P(N_{i_1}, \eta)}{P(N_{i_1}, z_0)} \right| < c. \tag{A6}
\]

This, together with Equation (A5) imply

\[
|P(N_{i_1} + N_{i_2}, z_0)\eta| < c|P(N_{i_1}, z_0)\eta| < c^2|\eta|. \tag{A7}
\]

Continuing this algorithm we obtain a sequence \( (t_n)_{n \geq 0} \), \( t_n \to \infty \) (with \( t_n = \sum_{j=1}^n N_j \) and \( t_0 = 0 \)) such that

\[
|P(t_n, z_0)\eta| < c^n|\eta| \quad \text{for all } n \geq 1.
\]

But since \( P(t_n, z_0)\eta = y(t) \), where \( z(t) = (x(t), y(t)) \) is the solution of Equation (4) with \( z(0) = z_0 \), we have that \(|y(t_n, z_0)| \to 0 \) as \( n \to \infty \). Also, since \( t_n \to \infty \), for all \( t \geq 0 \) there exists \( n \geq 0 \) such that \( t \in [t_n, t_{n+1}] \). Then we have

\[
|y(t, z_0)| = |y(t - t_n, z(t_n, z_0))| \to 0, \quad \text{as } t \to \infty, \tag{A8}
\]

where we used that \( t - t_n \in [0, N] \) and that \( z(t, z) \) is uniformly continuous in \( z \in B \), uniformly in \( t \in [0, \ldots, N] \). \( \blacksquare \)