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Global stability in discrete population models with delayed-density dependence

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Abstract

We address the global stability issue for some discrete population models with delayed-density dependence. Applying a new approach based on the concept of the generalized Yorke conditions, we establish several criteria for the convergence of all solutions to the unique positive steady state. Our results support the conjecture stated by Levin and May in 1976 affirming that the local asymptotic stability of the equilibrium of some delay difference equations (including Ricker's and Pielou's equations) implies its global stability. We also discuss the robustness of the obtained results with respect to perturbations of the model.

Keywords: Global stability; Population models; Conjecture of Levin and May; Yorke condition; Difference equations; Delay differential equations

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1. Introduction

The stability of equilibria is one of the most important issues in the studies of any model of single species population. The main conceptual result of these studies (both numerical and analytical) is the following folk theorem: '*The local stability of the unique positive equilibrium of a single species model implies its global stability*'. The practical importance of this result relies on the fact that it is much easier to perform the local analysis of the equilibrium than its global analysis. However, a rigorous mathematical proof of the above statement was found only in the simplest situations when populations are modelled by first order differential or difference equations (the paper [2] is a good source to find more details and references about this situation). In the case when the biological system is modelled by a higher order difference equation [13] or by a delay differential equation [7,19], only extensive numerical simulations [8,13] confirm the validity of the above affirmation; we do not know *any* case of analytical proof of it. This situation generated various stability conjectures: the most famous is the Wright conjecture (for the delayed logistic equation) waiting for an *affirmative* answer since 1955 (see, e.g., [12]). Similar conjectures were suggested by Smith for the Nicholson's blowflies model [14,16,21] (see also some discrete analogues in [3,6]), and by Levin and May in [13] for the Ricker delay difference equation and the Pielou delay difference equation (see also [11, Research Project 4.1.1] concerned with the latter equation).

Since anyone can readily find discrete or continuous dynamical systems having a unique stable positive equilibrium which does not attract all the trajectories, the following important question arises: *What characteristic feature of a single species population allows the perfect concordance between the local and global stability properties?* It is expected that the mathematical expression of this characteristic should possess some degree of robustness with respect to small perturbations of the model.

A possible approach to answer the above question was proposed independently in [2] (for first order difference population models) and in [16,17] (for a family of scalar functional differential equations). Its main ingredient consists in a comparison of the involved scalar non-linearity f with an appropriate Möbius (linear fractional) function r. In terms of [2], f should be *enveloped* by r, and it is required in [16] that f satisfy *the generalized Yorke condition* (see (H2) and (Y2) below). It is the purpose of this note to analyze some advances in the study of the above-mentioned Levin and May's conjecture proposed for delay difference equations; applying some techniques from [5,16,17], we obtain results which support an affirmative answer. Additionally, our global stability condition has a sort of weak autonomy with respect to the non-overlapping of generations postulate. It also shows a surprisingly strong robustness with respect to perturbations (not necessarily small or time-independent) of f.

2. Delay difference equations and EPCAs

There are various ways in which scalar delay difference equations (or, what is the same, scalar higher order difference equations) appear in the population biology. For example, they can be obtained as useful discrete versions of scalar delay differential equations; see [22,25] for more references and a discussion about the methods of discretization of continuous models. For example, if the population growth is described by a 1-periodic delay differential equation

$$x'(t) = x(t)f(t, x(t), x(t-1), \ldots, x(t-k)), \quad k \in \mathbb{N}, \tag{2.1}$$

then, assuming that the growth rate can be approximated as

$$f(t, x(t), x(t-1), \ldots, x(t-k)) \approx f(t, x(n), x(n-1), \ldots, x(n-k))$$

on the period intervals $[n, n+1)$, we get the following simplified version of (2.1):

$$x'(t) = x(t)f(t, x([t]), x([t-1]), \ldots, x([t-k])). \tag{2.2}$$

Here $[\cdot] : \mathbb{R} \to \mathbb{R}$ denote the greatest integer function: $[t] = n$, if $t \in [n, n+1)$. Eq. (2.2), which belongs to the class of delay differential equations with piecewise continuous argument (EPCAs, see [1]), can be easily integrated over intervals $[n, n+1)$ to get

$$x_{n+1} = x_n F_n(x_n, x_{n-1}, \ldots, x_{n-k}), \quad x_n > 0, \tag{2.3}$$

where we set $x_n = x(n)$ and $F_n(x_n, x_{n-1}, \ldots, x_{n-k}) = \exp(\int_0^1 f(s, x_n, x_{n-1}, \ldots, x_{n-k})\,\mathrm{d}s)$. In this way, the Ricker difference equation with delay

$$x_{n+1} = x_n \exp(\gamma - \alpha x_{n-k}), \quad \gamma, \alpha > 0, \ \ n = 0, 1, \ldots \tag{2.4}$$

can be obtained from the delayed logistic differential equation (also known as the Hutchinson equation (1948); see, e.g., [19]). The general form of Eq. (2.4) is

$$x_{n+1} = x_n F(x_{n-k}), \quad n = 0, 1, \ldots \tag{2.5}$$

and other important example of (2.5) is given by the Pielou equation [20]:

$$x_{n+1} = \frac{\lambda x_n}{1 + \alpha x_{n-k}}, \quad \lambda > 1, \quad \alpha > 0, \ \ n = 0, 1, \ldots \tag{2.6}$$

We notice that, for $k > 0$, Eq. (2.5) represents a significant simplification of (2.3); in general, the influence of other variables on the growth rate cannot be so underestimated. See, for example, the note [24], where the phenomenological model

$$x_{n+1} = x_n \exp(\gamma - \alpha x_n - \beta x_{n-1}), \quad \gamma, \alpha, \beta > 0, \ \ n = 0, 1, \ldots \tag{2.7}$$

was used instead of (2.4). Similarly, it is natural to consider the following non-autonomous version of (2.6)

$$x_{n+1} = \frac{\lambda x_n}{1 + \sum_{j=1}^{k} \alpha_{j,n} x_{n-j}}, \quad \alpha = \sum_{j=1}^{k} \alpha_{j,n}, \qquad n = 0, 1, \ldots \tag{2.8}$$

This form of the Pielou equation takes into account a possible influence of all generations on the growth rate and coincides with (2.6) if $\alpha_{k,n} = \alpha$ and $\alpha_{j,n} = 0$ for $j \neq k$. In the case when $\alpha_{0,n} = \alpha$ and $\alpha_{j,n} = 0$ for $j \neq 0$, Eq. (2.8) becomes the well known Beverton–Holt difference equation [7,22].

In all previous equations, due to the interpretation of x_n as a density of population, it was assumed that $x_n > 0$. Moreover, each considered model has a unique positive equilibrium x^*. A simple rescaling $z_n = x_n/x^*$ allows us to assume that $x^* = 1$ without loss of generality. Furthermore, we admit also negative values of the dependent variable after the change of variable $y_n = -\ln x_n$, which transforms Eq. (2.3) with strictly positive F_n into an equivalent difference equation

$$y_{n+1} = y_n - \ln F_n(\exp(-y_n), \exp(-y_{n-1}), \ldots, \exp(-y_{n-k})).$$

Finally, we observe that the latter equation (whose unique equilibrium is the trivial solution $y_n \equiv 0$) can be obtained from the EPCA

$$y'(t) = g(t, y([t]), y([t-1]), \ldots, y([t-k])), \tag{2.9}$$

where $g(t, \mathbf{z}) = g(t, z_0, z_1, \ldots, z_k) = -\ln F_n(e^{-z_0}, e^{-z_1}, \ldots, e^{-z_k})$ for $t \in [n, n+1), n \in \mathbb{N}$. Eq. (2.9) can also be deduced directly from Eq. (2.2).

3. The generalized Yorke condition and global stability

We will say that the positive equilibrium x^* of (2.3) is globally attracting if $\lim_{n\to+\infty} x_n = x^*$ for every sequence $\{x_n\}, x_n > 0$, satisfying (2.3). The positive equilibrium x^* of (2.3) is called locally asymptotically stable if it is stable and $\lim_{n\to+\infty} x_n = x^*$ for every solution x_n having the initial data sufficiently close to x^*. Finally, x^* is globally asymptotically stable [or simply globally stable] if it is stable and globally attracting.

The key assumption in our approach is that the generalized Yorke condition introduced in [16] (see also [5,17,23]) is satisfied by $g_n(\mathbf{z}) = -\ln F_n(e^{-z_0}, e^{-z_1}, \ldots, e^{-z_k})$. This condition is given in terms of the functional $\mathscr{M} : \mathbb{R}^{k+1} \to \mathbb{R}_+$ defined as $\mathscr{M}(\mathbf{z}) = \max\{0, \max_{i=0}^{k}\{z_i\}\}$. Below we list four hypotheses required in our main result:

(H1) There exists $\vartheta : \mathbb{R} \to \mathbb{R}_+$ such that $g_n(\mathbf{z}) \leqslant \vartheta(s)$ for every $z \in \mathbb{R}^{k+1}$, $\mathbf{z} = (z_0, \ldots, z_k)$, with $\min z_i \geqslant s$.

(H2) There are rational functions $r_n(x) = a_n x/(1 + bx)$, with $b \geqslant 0, a_n < 0$, such that

$$r_n(\mathscr{M}(\mathbf{z})) \leqslant g_n(\mathbf{z}) \leqslant r_n(-\mathscr{M}(-\mathbf{z})), \quad n \in \mathbb{N}, \tag{3.1}$$

where the first inequality holds for all $\mathbf{z} \in \mathbb{R}^{k+1}$, and the second one for all $\mathbf{z} \in \mathbb{R}^{k+1}$ such that $\min_i z_i > -b^{-1} \in [-\infty, 0)$.

(H3) If $\{z_n\}$ is a sequence of real numbers such that $\lim_{n\to\infty} z_n \neq 0$, then the series $\sum_{n=0}^{\infty} g_n(z_n, \ldots, z_{n-k})$ diverges.

(H4) For a_n as in (H2), there is $m_0 \geqslant k$ such that either

$$b > 0 \quad \text{and} \quad \sup_{m \geqslant m_0} \sum_{i=m}^{m+k} |a_i| \leqslant 3/2$$

or

$$b = 0 \quad \text{and} \quad \sup_{m \geqslant m_0} \sum_{i=m}^{m+k} |a_i| < 3/2.$$

We briefly explain the biological meaning of conditions (H1)–(H4) in regard to the population model (2.3). First, (H1) means that the growth rate F_n is *uniformly* positive, in the sense that $\inf_{n\geqslant 0} \inf\{F_n(x_0, \ldots, x_k) : 0 < x_i < s, i = 0, \ldots, k\} > 0$ for every fixed $s > 0$. Condition (H2) includes two natural ingredients to avoid destabilization of the model. First of them is the so-called negative feed-back condition with respect to the positive equilibrium, which in this case says that the population cannot increase (resp. decrease) after n generations if the size of the population in the previous $k+1$ generations $x_n, \dots, x_{n-k}$ was above (resp. below) the equilibrium. On the other hand, the restrictions on the size of F_n imposed by (H2) and (H4) prevent excessive growing of the solutions. See the last section for further discussions on (H2). Finally, condition (H3) says that the population cannot stabilize around a constant level different from the positive equilibrium. Actually, we do not need to require such a condition in the autonomous case, that is, when $F_n(x_0, \dots, x_k) \equiv F(x_0, \dots, x_k)$ is independent of n.

Now, we are ready to state our main result:

Theorem 3.1. *Let* $g_n(\mathbf{z}) = -\ln F_n(e^{-z_0}, e^{-z_1}, \dots, e^{-z_k})$, $n \in \mathbb{N}$, *satisfy* (H1)–(H4). *Then the positive equilibrium of the population modelled by (2.3) is globally attracting.*

To prove Theorem 3.1, we will use a result for functional delay differential equations (Theorem 3.2 below), which was established in [17] and improved in [5]. Such a theorem is a unified version of the celebrated 3/2—theorems by Wright and Yorke.

Let C be the space of continuous functions from $[-h, 0]$ to $\mathbb{R}, h > 0$, equipped with the norm $\|\varphi\| = \max_{-h \leqslant s \leqslant 0} |\varphi(s)|$. We consider the functional delay differential equation

$$y'(t) = w(t, y_t), \quad t \geqslant 0, \tag{3.2}$$

where as usual, for each $t \geqslant 0$, $y_t \in C$ is defined by $y_t(s) = y(t+s)$, $s \in [-h, 0]$.

Next we list the necessary hypotheses on the functional w, which were the motivation for (H1)–(H4).

(Y1) Function $w : \mathbb{R} \times C \to \mathbb{R}$ satisfies the Carathéodory condition. Moreover, for every $q \in \mathbb{R}$ there exists $\vartheta(q) \geqslant 0$ such that $w(t, \phi) \leqslant \vartheta(q)$ almost everywhere on $\mathbb{R}$ for every $\phi \in C$ satisfying the inequality $\phi(s) \geqslant q, s \in [-h, 0]$.

(Y2) There are a piecewise continuous function $\lambda : [0, +\infty) \to (0, +\infty)$ and a constant $b \geqslant 0$ such that, for $r(x) = -x/(1+bx)$, $x > -1/b$,

$$\lambda(t) r(\mathcal{M}(\phi)) = \frac{-\lambda(t)\mathcal{M}(\phi)}{1 + b\mathcal{M}(\phi)} \leqslant w(t, \phi) \leqslant \frac{\lambda(t)\mathcal{M}(-\phi)}{1 - b\mathcal{M}(-\phi)} = \lambda(t) r(-\mathcal{M}(-\phi)),$$

where the first inequality holds for all $\phi \in C$, and the second one for all $\phi \in C$ such that $\min_{s \in [-h,0]} \phi(s) > -b^{-1} \in [-\infty, 0)$. Here $\mathcal{M}(\phi) = \max\{0, \max_{s \in [-h,0]} \phi(s)\}$ is the Yorke functional (see, e.g., [12, Section 4.5]).

(Y3) $\int_0^{+\infty} w(s, p_s)\, ds$ diverges for every continuous $p(s)$ having non-zero limit at infinity.

(Y4) For $\lambda(t)$ as in (Y2), there is $T \geqslant h$ such that, for

$$\alpha := \alpha(T) = \sup_{t \geqslant T} \int_{t-h}^{t} \lambda(s)\, ds,$$

$$\alpha \leqslant 3/2 \text{ if } b > 0, \quad \text{and} \quad \alpha < 3/2 \quad \text{if } b = 0.$$

Notice that (Y3) implies that $y(t) \equiv 0$ is the unique equilibrium of the equation. We recall that $w(t, \phi)$ is a Carathéodory function if it is measurable in t for each fixed ϕ, continuous in ϕ for each fixed t, and for any fixed $(t, \phi) \in \mathbb{R} \times C$ there is a neighborhood $V(t, \phi)$ and a Lebesgue integrable function m such that $|w(s, \psi)| \leqslant m(s)$ for all $(s, \psi) \in V(t, \phi)$ (see [9, p. 58]).

Theorem 3.2. ([5, Theorem 2.5]) *Assume that w satisfies* (Y1)–(Y4). *Then all solutions of* (3.2) *converge to zero as $t \to +\infty$.*

Proof of Theorem 3.1. With Eq. (2.3), we have already associated Eq. (2.9), which can be written as (3.2) with $w : \mathbb{R} \times C([-k-1, 0], \mathbb{R}) \to \mathbb{R}$ defined as

$$w(t, \phi) = g(t, \phi(-\{t\}), \phi(-\{t\} - 1), \ldots, \phi(-\{t\} - k)).$$

Here, $\{t\} = t - [t] \in [0, 1)$. It is easy to check that the above w satisfies (Y2) with the piecewise constant function $\lambda(t) = |a_n|$, $t \in [n, n+1)$. Hence, since

$$\alpha = \sup_{t \geqslant m_0} \int_{t-k-1}^{t} \lambda(s)\,\mathrm{d}s = \sup_{m \geqslant m_0} \sum_{i=m}^{m+k} |a_i|,$$

(Y4) follows from (H4). Conditions (Y1) and (Y3) are derived from (H1) and (H3), respectively. Thus, Theorem 3.2 ensures the convergence of all solutions of (2.9) to zero. Let now $\{x_n\}_{n \geqslant -k}$ be a solution to (2.3). Consider the initial value problem for (2.9), with $y(s) = \psi(s)$, $s \in [-k-1, 0]$, where $\psi \in C([-k-1, 0], \mathbb{R})$ is such that $\psi(j) = -\ln x_j$ for all $j = -k, -k+1, \ldots, 0$. An elementary analysis shows that, in this case, $x_n = \exp(-y(n))$ for every $n \geqslant 0$. Hence, $\lim_{n \to +\infty} x_n = 1$ for every solution x_n of (2.3) and Theorem 3.1 is proved. □

4. Stability of $x_{n+1} = x_n F(x_{n-k})$

In this section, we investigate Eq. (2.5) in more detail, in order to shed some new light on the Levin and May's conjecture mentioned in the introductory part. We consider a more general equation

$$x_{n+1} = x_n F\left(\sum_{i=0}^{k} \alpha_i x_{n-i}\right), \quad n = 0, 1, \ldots, \tag{4.1}$$

where $\alpha_i \geqslant 0$, $\sum_{i=0}^{k} \alpha_i = 1$. We will assume that $F : [0, \infty) \to (0, \infty)$ is continuous, non-increasing, and there exists a unique $x^* > 0$ such that $F(x^*) = 1$. Without loss of generality, we can set $x^* = 1$.

In this case it is not difficult to check that conditions (H1) and (H3) automatically hold for

$$g_n(z_0, z_1, \ldots, z_k) = -\ln F\left(\sum_{i=0}^{k} \alpha_i \mathrm{e}^{-z_i}\right),$$

since Eq. (4.1) is autonomous, F is continuous, and $F(x) = 1$ only for $x = 1$. On the other hand, one can check that (H2) holds for g_n if $g(x) = -\ln F(\mathrm{e}^{-x})$ satisfies (H2) for some rational function $r(x) = ax/(1 + bx)$, $a < 0$, $b \geqslant 0$. Notice that, in this case, $\mathcal{M}(x) = \max\{0, x\} = x^+$, for all $x \in \mathbb{R}$.

The above discussion allows us to state the following consequence of Theorem 3.1:

Theorem 4.1. *Let $g(x) = -\ln F(e^{-x})$ satisfy* (H2). *Then the positive equilibrium of* (4.1) *is globally attracting if either $b > 0$ and $|a|(k+1) \leqslant 3/2$, or $b = 0$ and $|a|(k+1) < 3/2$.*

Remark 4.2. The conclusion of Theorem 4.1 remain valid if, instead of $g(x)$, condition (H2) holds for $\hat{g}(x) = \ln F(e^x)$. For it, we only have to use the change of variables $y_n = \ln x_n$ instead of $y_n = -\ln x_n$.

On the other hand, for the particular case of Eq. (2.5) (i.e., (4.1) with $\alpha_k = 1$, $\alpha_i = 0$, $i = 0, \ldots, k-1$), the monotone character of F is not necessary.

Since in the applications it may be difficult to check (H2) for either g or $\hat{g}$ directly, we give two results which can simplify this task.

First one make use of the so-called Schwarzian derivative, which is defined for a function $g \in C^3(\mathbb{R}, \mathbb{R})$ by

$$(Sg)(x) = \frac{g'''(x)}{g'(x)} - \frac{3}{2}\left(\frac{g''(x)}{g'(x)}\right)^2,$$

for all $x \in \mathbb{R}$ where $g'(x) \neq 0$. Let us introduce the following assumptions:

(A1) $g(0) = 0, g'(x) < 0$ for all $x \in \mathbb{R}$ and g is bounded below.
(A2) $(Sg)(x) < 0$ for all $x \in \mathbb{R}$.

It follows from Lemma 2.1 in [15] that, if g satisfies (A1) and (A2) and $g''(0) \geqslant 0$, then (H2) holds with $a = g'(0)$ and $b = -g''(0)/(2g'(0))$. Notice that $\hat{g}''(0) \geqslant 0$ if $g''(0) \leqslant 0$, and $\hat{g}$ satisfies (A1) and (A2) if g fulfills (A1) and (A2) and $g''(0) < 0$ (see [15, Corollary 2.2]). Hence, we have the following.

Corollary 4.3. *Let $g(x) = -\ln F(e^{-x})$ satisfy (A1) and (A2) and either $g''(0) \neq 0$ and $|g'(0)|(k+1) \leqslant 3/2$, or $g''(0) = 0$ and $|g'(0)|(k+1) < 3/2$. Then the positive equilibrium of (4.1) is globally attracting.*

Remark 4.4. Since $F(1) = 1$, $g'(x) = F'(e^{-x})e^{-x}/F(e^{-x})$, and $g(+\infty) = -\ln(F(0))$, it follows that g satisfies (A1) whenever $F'(x) < 0$ for all $x > 0$.

Sometimes, function $g(x) = -\ln F(e^{-x})$ takes a rather complicated form, which makes more difficult to check the hypotheses of Theorem 4.1 and Corollary 4.3. Next result shows that in some cases we can check those conditions for the simpler function $\widetilde{F}(x) = F(x+1) - 1$, obtained by shifting the equilibrium $x = 1$ to the origin. Notice that, due to Lemma 2.1 from [15], $\widetilde{F}$ satisfies (H2) if F is decreasing, $F(0) > 1$, and $(SF)(x) < 0$ for $x \geqslant 0$.

Proposition 4.5. *Let $\widetilde{F}(x) = F(x+1) - 1$ satisfy (H2) with some $a \in (-1, 0)$ and $b + a \geqslant 0$, $1 - a - 2b > 0$ (so that $b \in (0, 1)$). Then the positive equilibrium of (4.1) is globally attracting if $|a|(k+1) \leqslant 3/2$.*

Proof. We will show that $g(x) = -\ln F(e^{-x})$ also meets (H2) with the same a and $b_1 = (1 - a - 2b)/2$.

Set $R(y) = ay/(1 + by)$. Due to our assumptions,

$$F(y) \geqslant R(y-1) + 1 > 0, \quad y \geqslant 1,$$
$$F(y) \leqslant R(y-1) + 1, \quad y \in (1 - b^{-1}, 1).$$

Therefore $(-\ln(F(e^{-x})) - w(x))x \geqslant 0$, where $w(x) = -\ln(R(e^{-x} - 1) + 1)$. Now, it suffices to prove the negativity of the Schwarzian of $w(x)$, because this implies (see [15]) that $(w(x) - ax/(1 + b_1x))x > 0$, $x \neq 0$ with $a = w'(0)$, $b_1 = -0.5w''(0)/w'(0) = (1 - a - 2b)/2$. Using the chain rule formula for the Schwarz derivative, we have

$$(Sw)(x) = (S[f \circ v \circ h])(x) = (Sf)(v(z))(v_z(z)z_x)^2 + (Sv)(z)(h'(x))^2 + (Sh)(x)$$

with $f(y) = -\ln y, y = v(z) = R(z) + 1, z = h(x) = e^{-x} - 1$. Since $(Sf)(y) = 1/(2y^2)$, $(Sv)(z) = 0$, $(Sh)(x) = -1/2$, we get

$$(Sw)(x) = \frac{1}{2}\left(\frac{R_z(z)(z+1)}{(R(z)+1)}\right)^2 - \frac{1}{2} = \frac{1}{2}\left(\frac{a(1+z)}{(1+bz)(1+z(a+b))}\right)^2 - \frac{1}{2} < 0, \tag{4.2}$$

since the squared expression in (4.2) is less than 1. Proposition 4.5 is proved. □

Next we apply our results to the models (2.4) and (2.6). Notice that in both cases F is smooth and hence we can apply the following asymptotic stability criterion from [13].

Proposition 4.6. *The positive equilibrium x^* in (2.5) is asymptotically stable if*

$$x^*|F'(x^*)| < 2\cos\left(\frac{\pi k}{2k+1}\right). \tag{4.3}$$

Remark 4.7. Since $|g'(0)| = x^*|F'(x^*)|$, and (4.3) holds if $(k+1)x^*|F'(x^*)| \leqslant 3/2$, Corollary 4.3 provides sufficient conditions for the global stability in (2.5) when the non-linearity F is smooth.

For model (2.4), it is easy to check that $g(x) = \gamma(e^{-x} - 1)$, and hence (A1) and (A2) are very easy to verify. In particular, $(Sg)(x) = -1/2 < 0$ for all $x \in \mathbb{R}$. Since $g'(0) = -\gamma$, $g''(0) = \gamma > 0$, Corollary 4.3 and Remark 4.2 ensure that x^* is globally stable for (2.4) if $\gamma(k+1) \leqslant 3/2$, which improves condition $\gamma(k+1) \leqslant 1$ established in [10]. In the case of model (2.6), function $\widetilde{F}$ is a rational function $\widetilde{F}(x) = ax/(1+bx)$, with $a = (1-\lambda)/\lambda \in (-1,0)$ and $b = -a \in (0,1)$. Hence, an immediate application of Proposition 4.5 ensures that the equilibrium $x^* = (\lambda - 1)/\alpha$ is globally attracting if $(1 - 1/\lambda)(k+1) \leqslant 3/2$. Moreover, Proposition 4.6 applies and x^* is actually globally stable.

Notice that our global stability condition for (2.4) and (2.6) can be stated as

$$x^*|F'(x^*)| \leqslant \frac{3}{2(k+1)}, \tag{4.4}$$

while the condition in [10] is

$$x^*|F'(x^*)| \leqslant \frac{1}{k+1}. \tag{4.5}$$

Taking into account the relations

$$\frac{3}{2(k+1)} < 2\cos\left(\frac{\pi k}{2k+1}\right) \leqslant \frac{2}{k+1}, \quad k \geqslant 1 \tag{4.6}$$

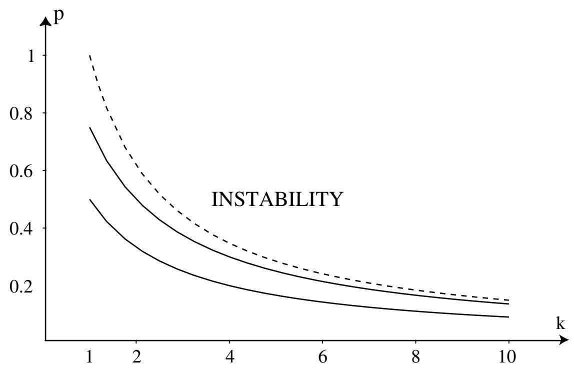

Fig. 1. Border of the local stability region (dashed line) against the global stability regions given by (4.4) and (4.5) ($p = x^*|F'(x^*)|$).

and Fig. 1, where the good agreement between the stability conditions given in Corollary 4.3 and Proposition 4.6 is shown, one is tempted to suggest the following generalization of May and Levin's conjecture:

Conjecture 4.8. *Assume that $F \in C^3([0,\infty),(0,\infty))$ is strictly decreasing, $F(0) > 1 = F(x^*)$, and function $g(x) = -\ln F(e^{-x})$ has negative Schwarz derivative for all $x \in \mathbb{R}$. Then the local asymptotic stability of the equilibrium x^* of (2.5) implies its global asymptotic stability.*

5. A possible generalization of Theorem 4.1

In this section, we suggest a first step in the direction to justify further (or disprove) Conjecture 4.8. In concrete, we propose to investigate if the stability condition (4.4) established for (2.4) and (2.6) can be replaced by

$$x^*|F'(x^*)| < \frac{3}{2(k+1)} + \frac{1}{2(k+1)^2}, \tag{5.1}$$

which is a better approximation to (4.3). Notice that, for $k \geqslant 1$,

$$\frac{3}{2(k+1)} < \frac{3}{2(k+1)} + \frac{1}{2(k+1)^2} < 2\cos\left(\frac{\pi k}{2k+1}\right) = \frac{\pi}{2(k+1)} + \mathrm{O}\left(\frac{1}{k+1}\right)^2. \tag{5.2}$$

Another motivation to consider such an expression is the following: Erbe et al. [4] proved that all solutions of the difference equation

$$x_{n+1} - x_n = a_n x_{n-k}, \tag{5.3}$$

where $\{a_n\}$ is a sequence of non-positive numbers, converge to zero if

$$\limsup_{n\to\infty} \sum_{i=n-k}^{n} |a_n| < \frac{3}{2} + \frac{1}{2(k+1)} \quad \text{and} \quad \sum_{n=0}^{\infty} |a_n| = \infty. \tag{5.4}$$

The result by Erbe et al. was generalized in [18] to the non-linear difference equation

$$x_{n+1} - x_n = a_n f(x_{n-k}), \tag{5.5}$$

where f is a continuous function satisfying the negative feed-back condition $xf(x) < 0$ for all $x \neq 0$, and f is a sub-linear function: $|f(x)| < x, x \neq 0$. Although the non-linearities corresponding to models (2.4) and (2.6) do not satisfy this last condition, we should expect that the result remain true for Eq. (5.5) with f satisfying (H1) and (H3). See [5,16], where a similar generalization was made for delay differential equations. Summing up, we guess that the following result is true:

Open problem. Show that all solutions of (5.5) converge to zero if (H1) and (H3) hold, $f'(0) = -1$, and $\{a_n\}$ satisfies (5.4).

Let us observe that, for $|a_n| \equiv p > 0$, condition (5.4) reads

$$p < \frac{3}{2(k+1)} + \frac{1}{2(k+1)^2}.$$

Hence, if the answer to the problem is positive, the global stability condition (4.4) is improved up to (5.1).

6. Conclusions

The dynamics of population models is the basis of many studies on difference equations (discrete models) and delay-differential equations (continuous models). It is a common feature among many of them that there exists a unique positive equilibrium x^* which losses its asymptotic stability with the appearance of non-trivial periodic solutions (either in a period-doubling bifurcation in the discrete case, or in a Hopf bifurcation in the continuous case). However, the global dynamics for the values of the parameters for which the equilibrium is stable are not completely understood. For example, for the continuous delayed logistic equation, the Wright conjecture (1955), saying that the equilibrium is globally stable whenever it is locally stable, is still an open problem.

In this note, we have given new results which support the positive answer to this open problem and other related conjectures (in particular, the one proposed by Levin and May in 1976). Moreover, we see that a common property, which seems to be the responsible for this agreement between the local and global properties, is that the non-linearity satisfies the generalized Yorke condition. From the biological point of view, the robustness of hypothesis (H2) cannot be underestimated: it assures that even relatively large perturbations cannot change drastically the globally attracting behavior of the equilibrium in a model satisfying (H2). Indeed, what (H2) is saying is that the unique property of the involved non-linearity which has real importance is the position of its graph with respect to some linear fractional function, and this property is robust. For example, by Corollary 4.3, function $g(x) = \gamma(\exp(-x)-1)$ (obtained from the normalized equation (2.4)) is enveloped by $r(x) = -2\gamma x/(2 + x)$. Since the global stability result holds for $\gamma \leqslant 3/(2(k + 1))$, we can see that significant modifications in the form of g, whenever they occur outside a small

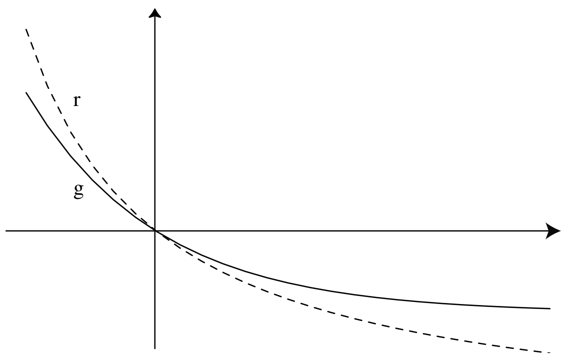

Fig. 2. Graphs of $g(x) = \gamma(\exp(-x)-1)$ and its rational approximation.

neighborhood of $x = 0$, do not affect our basic property (H2): it is sufficient that the perturbed function remain enveloped by

$$r(x) = \frac{-3x}{(k+1)(2+x)}.$$

See Fig. 2, where, for $k = 1$, we plot the graphs of $g(x) = \gamma(\exp(-x)-1)$, with $\gamma = 0.6 < 3/4$, and the rational function $r(x) = -1.5x/(2 + x)$. Recall that $x = 0$ here corresponds to the positive steady state x^* in (2.4).

Furthermore, the use of the Yorke functional in the statement of (H2) provides a kind of weak independence of the global stability property from the non-overlapping of generations postulate. In this respect, see again the statement of Theorem 4.1, which does not depend on the choice of the weights α_j in (4.1). As it was noticed in recent papers [5,14–16,23] (see also [2]), the property (H2) is shared by many celebrated population models and is intimately linked with the negative Schwarzian property (notice that linear fractional functions have zero Schwarzian). As a result of our discussion, we have formulated Conjecture 4.8 and indicated another open problem whose solution can be seen as the first step in the direction to solve (justify further) the conjecture.

Finally, we show that the 'magic number' 3/2 (already found in the fifties by Wright and Myshkis in delay differential equations) plays an important role in the stability results, in special when we consider equations with variable coefficients (2.3) and (5.5).

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