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LOCAL STABILITY IMPLIES GLOBAL STABILITY IN SOME ONE-DIMENSIONAL DISCRETE SINGLE-SPECIES MODELS

Eduardo Liz

Departamento de Matemática Aplicada II, E.T.S.I. Telecomunicación
Universidad de Vigo, Campus Marcosende, 36280 Vigo, Spain

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Abstract. We prove a criterion for the global stability of the positive equilibrium in discrete-time single-species population models of the form $x_{n+1} = x_n F(x_n)$. This allows us to demonstrate analytically (and easily) the conjecture that local stability implies global stability in some well-known models, including the Ricker difference equation and a combination of the models by Hassel and Maynard Smith. Our approach combines the use of linear fractional functions (Möbius transformations) and the Schwarzian derivative.

1. **Introduction.**

One-dimensional dynamical systems are an appropriate mathematical tool to model the behaviour of populations with nonoverlapping generations. Since the early work of Ricker (1954) and Beverton and Holt (1957), among others (see, e. g., [10, Chapter 9]), extensive research was done by many authors, including aspects as stability , periodic solutions, and chaotic behaviour. The papers by R. M. May *et al.* ([4] and references therein) in the seventies and classical monographs by Maynard Smith and Pielou have served as an important impulse for further research.

In this note, we will focus our attention in one-dimensional models governed by a difference equation

$$x_{n+1} = f(x_n)\,, \quad n = 0, 1, \ldots, \tag{1.1}$$

where f satisfies the following usual assumption in population dynamics:

Assumption 1.1. [10, Assumption 9.4, p. 86] $f : (0,\infty) \to (0,\infty)$ is continuous, has a unique fixed point $\bar{x}$, and is bounded on $(0, \bar{x}]$. Furthermore, $f(x) > x$ for $x < \bar{x}$, and $f(x) < x$ for $x > \bar{x}$.

After normalization, we can always assume that $\bar{x} = 1$. The study of the local asymptotic stability of $\bar{x}$ is simple; if f is differentiable, it is well known that the equilibrium $\bar{x} = 1$ is asymptotically stable if $|f'(1)| < 1$, and it is unstable if $|f'(1)| > 1$. If only continuity is assumed, several criteria for the local asymptotic stability of the equilibrium are given in [8, Theorems 2.1.1 and 2.1.2]. In general, it is much more complicated to investigate if $\bar{x}$ is globally stable, that is, if it is stable and globally attracting. We say that $\bar{x}$ is globally attracting if all solutions

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$\{x_n\}$ of (1.1) converge to $\bar{x}$ as $n \to \infty$. Notice that, under Assumption 1.1, a globally attracting fixed point for (1.1) is always globally stable (see, e. g., [1] and [8, Corollary 2.1.3]). Moreover, $\bar{x}$ is a global attractor for (1.1) if and only if it is the unique fixed point of function $f^2 = f \circ f$ ([10, Theorem 9.6], see also [1, 8]). However, this interesting result is not so easy to apply, and for important examples of (1.1) there is still a gap between the local stability criteria –given in terms of the parameters involved in the model– and the sufficient conditions for the global stability. The main motivation for writing this note was to fill this gap at least for some well-known population models, showing that the popular statement

$$\text{“L. A. S.} \implies \text{G. A. S.”} \tag{1.2}$$

(supported by extensive numerical studies [4, 10]) is true, and it can be proved analytically in a simple way. Indeed, many authors have observed that (1.2) (that is, *the local asymptotic stability of the equilibrium implies its global asymptotic stability*) is a common property shared by the most popular discrete single-species models (I have read this observation for the first time in the paper [4] by Levin and May). In some cases, this property may be demonstrated by elementary calculus; for other situations, several tools have proved to be effective. See the discussion in [1, 2, 3, 4] and some related results in [10]. Of special interest are the recent results by Cull *et al.* [2, 3], where (1.2) was proved for seven different population models (already listed in [1]) by using a new approach based on “enveloping” (we shall be more precise in Section 2). Nevertheless, for some cases either this method is not effective, or its application is very complicated. We have found two examples in the recent book by H. R. Thieme [10]; using our approach, we prove in Section 3 that (1.2) is also true for them. The first one is the Ricker difference equation

$$x_{n+1} = x_n \left(q + \gamma e^{-x_n} \right), \quad n = 0, 1, \ldots, \tag{1.3}$$

where $q \in [0, 1)$, $\gamma > 0$. Cull [1, 2] investigated this equation for $q = 0$, $\gamma = 1$. For the general case, it is claimed in [10] that there is a gap between the local stability condition $\bar{x}(1 - q) \leq 2$, where $\bar{x} = \ln(\gamma/(1 - q))$ is the positive equilibrium, and the known global stability conditions.

The second one is a combination of the models by Hassel and Maynard Smith

$$x_{n+1} = \frac{a x_n}{\left(1 + b x_n^{\xi}\right)^{\zeta}}, \quad n = 0, 1, \ldots, \tag{1.4}$$

where $a > 1$, $b, \xi, \zeta > 0$. In [10], a sufficient condition for the global stability of the positive equilibrium is given, but it is far from being sharp. On the other hand, (1.4) contains as particular cases models **VI** and **VII** in [3]; we notice that the authors needed to split the study of global stability for each of them in several different cases, some of them rather complicated. We will show that (1.2) can be proved for (1.4) in an unified and surprisingly simple way using our approach.

Our main results are stated and proved in the second section. The key ideas were used recently in the research of global stability in a different setting. One of them is the relation between the sign of the Schwarzian derivative of a function and the position of its graph with respect to the one of a Möbius transformation; it was introduced in [5] to address the global stability of a delay differential equation. The other one is a generalization of a celebrated condition by Yorke used to obtain uniform asymptotic stability in functional differential equations; such a generalization was introduced in [6], and it was also employed in the setting of difference equations in [7, 11]. As we will see, it is closely related to the above mentioned Cull's idea of enveloping.

Section 3 is devoted to show the applicability of our results, in particular for equations (1.3) and (1.4). Finally, in Section 4 we emphasize that property (1.2) was also suggested by Levin and May [4] for difference-delay equations

$$x_{n+1} = x_n F(x_{n-k}), \quad n = 0, 1, \dots, \tag{1.5}$$

with $k > 0$. For this case, it seems to be much more difficult to prove analytically such a property; however, some recent results [7, 11] suggest that it is true. We formulate a related conjecture in this direction.

2. **Enveloping and Schwarzian derivative: Main results.** One of the tools used to prove global stability in difference equations is the Schwarzian derivative, which was first introduced into the study of one-dimensional dynamical systems by D. Singer in 1978 [9]. We recall that the Schwarzian derivative of a C^3-map f is defined by

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

whenever $f'(x) \neq 0$. The following proposition can be deduced from Singer's results; its proof is completely analogous to the one of [6, Proposition 3.3], which was given for a map defined on a compact interval.

Proposition 2.1. *Let Assumption 1.1 hold, and suppose f is C^3 and has at most one critical point x^* (maximum). If $|f'(\bar{x})| \leq 1$, and $(Sf)(x) < 0$ for all $x \neq x^*$, then $\bar{x}$ is globally stable.*

However, in some important models, either the Schwarzian of f is not negative everywhere or it is difficult to evaluate its sign. For instance, this actually happens for models (1.3) and (1.4). In some cases, it is still possible to prove the global stability of the equilibrium by using a method recently developed by Cull and Chafee [3]. It is based on the general principle *"enveloping implies G. A. S."*. We provide a brief description of the method; for more details, see [2, 3]. For simplicity, we assume that Assumption 1.1 holds, although Cull's method is more general. For $\alpha \in [0, 1)$, consider the linear fractional function

$$\phi_\alpha(x) = \frac{1 - \alpha x}{\alpha - (2\alpha - 1)x}. \tag{2.1}$$

Assuming (after normalization if necessary) that $\bar{x} = 1$ is the positive equilibrium of f, we say that ϕ *envelops* f if $\phi(x) > f(x)$ on $(0, 1)$, and $\phi(x) < f(x)$ for all $x > 1$. The following result was stated in [2].

Proposition 2.2. [2, Corollary 2] *Assume that ϕ_α envelops f for some $\alpha \in [0, 1)$. Then the positive equilibrium of (1.1) is globally stable.*

Cull and Chafee [3] use this result and some remarks to prove global asymptotic stability for seven different models. However, this task is not easy, and they recognize that despite the simple formulation of Proposition 2.2, the parameter α in (2.1) must be adjusted for each particular model, and even the parameter changes in some cases depending of the parameters involved in the model. They suggest that this parameter dependence might be the reason why this simple criterion has not been discovered before. The writing of the present note was intended not only as an attempt to get a criterion for G. A. S. easier to use, but also to make clear that the parameter α is not so difficult to find; we show that under some conditions (met by the examples in the Introduction) α has a clear meaning and it is easy to determine it.

Before formulating our main results, we rewrite Equation (1.1) in the form

$$x_{n+1} = x_n F(x_n)\,, \quad n = 0, 1, \ldots . \tag{2.2}$$

In fact, this is an usual formulation in population dynamics (see, e.g., [4]). Notice that the unique positive equilibrium solves equation $F(\bar{x}) = 1$. The change of variables

$$y_n = -\ln\left(\frac{x_n}{\bar{x}}\right) \tag{2.3}$$

transforms (2.2) into

$$y_{n+1} - y_n = g(y_n)\,, \quad n = 0, 1, \ldots, \tag{2.4}$$

where $g(y) = -\ln(F(\bar{x}e^{-y}))$. Notice that, after (2.3), the equilibrium $\bar{x}$ becomes $y = 0$, and y_n takes negative values for $x_n > \bar{x}$. It is obvious that $\bar{x}$ is G. A. S. for (2.2) if and only if 0 is G. A. S. for (2.4).

We can now state our main result. The idea of the proof is taken from [11], where the authors consider the non-autonomous delayed difference equation

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

with $k \geq 1$. Notice that equation (2.4) is essentially the autonomous version of (2.5) with $k = 0$. We emphasize that, in contrast with the complicated analysis necessary to address the global stability in Equation (2.5), the proof of Theorem 2.3 is based on rather simple arguments.

Theorem 2.3. *Assume that there exists a positive constant b such that*

$$r(y) \leq g(y) < 0\,,\ \forall\, y > 0 \quad \text{and} \quad 0 < g(y) \leq r(y)\,,\ \forall\, y \in (-1/b, 0)\,, \tag{2.6}$$

where $r(y) = -2y/(1 + by)$.

Then the equilibrium $y = 0$ is globally stable for (2.4).

Proof. Our proof starts with the observation that it is enough to consider the case $b = 1$ in (2.6). Indeed, the change of variables $t_n = by_n$ transforms (2.4) into $t_{n+1} - t_n = h(t_n)$, where h satisfies (2.6) with $b = 1$. Hence, we can assume that

$$r(y) = \frac{-2y}{1+y}\,.$$

Suppose the assertion of the theorem is false. Then, there must be a cycle of prime period two of function $y + g(y)$, that is, there exist real numbers $m < 0$, $M > 0$ such that $m = M + g(M)$, $M = m + g(m)$. We will use the auxiliary function $R : (-1/2, \infty) \to (-1/2, \infty)$ defined by

$$R(x) = \frac{-x}{1+2x}\,. \tag{2.7}$$

The following properties are very easy to check.

$$x + r(x) > R(x)\,,\ \forall\, x > 0 \quad ; \quad x + r(x) < R(x)\,,\ \forall\, x \in (-1/2, 0)\,; \tag{2.8}$$

$$R(R(x)) = x\,,\ \forall\, x > -1/2 \quad ; \quad R \text{ is decreasing on } (-1/2, \infty)\,. \tag{2.9}$$

By (2.6) and (2.8),

$$m = M + g(M) \geq M + r(M) > R(M)\,. \tag{2.10}$$

In particular, $m > -1/2$ and we can define $r(m), R(m)$. Thus, again by (2.6) and (2.8),

$$M = m + g(m) \leq m + r(m) < R(m)\,. \tag{2.11}$$

From (2.9), (2.10) and (2.11), we get

$$M < R(m) < R(R(M)) = M,$$

a contradiction proving the theorem. □

Remark 2.4. Before formulating a useful corollary, we list several comments.

(a) The statement of Theorem 2.3 has a close relation with the one of Proposition 2.2. Indeed, if we translate the equilibrium $\bar{x} = 1$ to $x = 0$ in (2.1), it takes the form $\phi(y) = -y/(1+by)$, with $b = (1-2\alpha)/(1-\alpha)$. Compared with Cull's results, Theorem 2.3 has the particularity to work with function g instead of f. We will show in Section 3 how useful this fact is in the applications.

(b) The conclusion of Theorem 2.3 also holds for $b = 0$. In this case, (2.6) is satisfied with $r(x) = -2x$. Notice that Equation (2.4) can be written in the form

$$y_{n+1} = \bar{g}(y_n),$$

with $\bar{g}(y) = y + g(y)$, in such a way that $\phi(x) = -x$ envelops $\bar{g}$. Accordingly, the result follows from Proposition 2.2.

(c) As we will see, the restriction $b > 0$ is not very important in the applications. If $b < 0$, then we make the change of variables $z_n = -y_n$, which transforms Equation (2.4) into

$$z_{n+1} - z_n = G(z_n)\,, \quad n = 0, 1, \ldots, \tag{2.12}$$

with $G(z) = -g(-z)$.

Now, as remarked by Cull [2], it is not easy to find the linear fractional function r in (2.6) for a model depending on several parameters. Some alternative methods are discussed in [3]. We show that the Schwarzian derivative plays an important role in simplifying this task. First, let us observe that in many important models of the form (2.2) function F has the following property:

$$F : [0, \infty) \to (0, \infty) \quad \text{is differentiable and} \quad F'(x) < 0 \quad \text{for all} \quad x > 0. \tag{2.13}$$

For example, (2.13) holds for the models (1.3) and (1.4) mentioned in the introduction. Next, from (2.13) it follows that the function $g(y) = -\ln(F(\bar{x}e^{-y}))$ involved in (2.4) satisfies the following properties:

$$g'(x) < 0 \quad \text{for all} \quad x \in \mathbb{R} \;\; ; \;\; xg(x) < 0 \quad \text{for all} \quad x \neq 0, \quad \text{and} \quad g \text{ is bounded below.} \tag{2.14}$$

Then, the following result from [5] will play a key role in the applications.

Proposition 2.5. *Assume that g is a C^3 function satisfying (2.14). If $g''(0) \geq 0$, $|g'(0)| \leq 2$, and $(Sg)(x) < 0$ for all $x \in \mathbb{R}$, then g satisfies (2.6) with $b = -g''(0)/(2g'(0))$.*

Remark 2.6. The relation between the Schwarzian derivative and the Möbius transformations is not surprising; in fact, the well-known property that the Schwarzian derivative of Möbius transformations is zero at every point is very important in proving Proposition 2.5 (see [5] for more details).

The following consequence of Theorem 2.3 and Proposition 2.5 is very useful in the applications.

Corollary 2.7. *Assume that F satisfies (2.13) and the function $g(y) = -\ln(F(\bar{x}e^{-y}))$ has negative Schwarzian derivative everywhere. Then the local asymptotic stability of the unique positive equilibrium $\bar{x}$ in equation*

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

implies its global stability.

Proof. Let us assume first that $g''(0) \geq 0$. Since F satisfies (2.13), then g satisfies (2.14). Thus, since $(Sg)(y) < 0$ for all $y \in \mathbb{R}$, it follows from Proposition 2.5 that g satisfies (2.6) with $b = -g''(0)/(2g'(0)) > 0$ if $|g'(0)| \leq 2$, or, equivalently, $\bar{x}|F'(\bar{x})| \leq 2$. By Theorem 2.3, we conclude that $\bar{x}$ is globally stable if $\bar{x}|F'(\bar{x})| \leq 2$. Since $\bar{x}$ is unstable when $\bar{x}|F'(\bar{x})| > 2$, the statement of the corollary is proven in the case $g''(0) \geq 0$. If $g''(0) < 0$, as noticed in Remark 2.4, the change of variables $z_n = -y_n$ transforms (2.4) into (2.12), with $G(z) = -g(-z)$. It is easy to check that $(SG)(z) = (Sg)(-z) < 0$, and $G'(z) = g'(-z) < 0$ for all $z \in \mathbb{R}$. Moreover, $G''(0) = -g''(0) > 0$, and $zG(z) = -zg(-z) < 0$ for all $z \neq 0$. To apply the first part of the proof, it only remains to show that G is bounded below. This is a consequence of Corollary 2.2 in [5], namely, if g satisfies (2.14), $(Sg)(y) < 0$ for all $y \in \mathbb{R}$, and $g''(0) < 0$, then g is bounded on $\mathbb{R}$. $\square$

Let us observe that, under conditions of Corollary 2.7, we have proved the global asymptotic stability of $\bar{x}$ not only for the hyperbolic case $|g'(0)| < 2$, but also for the nonhyperbolic case $g'(0) = -2$.

An important point to note here is that we do not need to find explicitly the constant b (equivalently α in Cull's results) to apply Corollary 2.7. In the next section, we show that it is not hard to deal with the Schwarzian derivative of g in the models under consideration. Thus, we are able to solve the conjectures in [10, Chapter 9].

Remark 2.8. Corollary 2.7 shows that Conjecture 4.8 in [7] is true for $k = 0$.

3. **Applications.**

In this section, we apply Corollary 2.7 to some important discrete-time population models satisfying Assumption 1.1.

Example 3.1. Let us start considering the Ricker difference equation (1.3). Assuming that $q + \gamma > 1$, this equation has a positive equilibrium $\bar{x} = \ln(\gamma/(1-q))$. After normalization, we can consider the equivalent equation

$$x_{n+1} = x_n \left(q + (1-q)e^{r(1-x_n)} \right)\,, \quad n = 0, 1, \ldots, \tag{3.1}$$

where $q \in [0, 1)$, $r = \bar{x}$. Thus the equilibrium $x = 1$ in (3.1) is locally asymptotically stable if and only if

$$(1-q)r \leq 2\,. \tag{3.2}$$

In [10], it is proved that this positive equilibrium is globally stable if

$$r \leq 2 + \ln\left(1 + \frac{2q}{1-q}\right)\,, \tag{3.3}$$

so there is a gap between the conditions for local and global stability. This gap is larger for larger q. We use Corollary 2.7 to fill this gap, that is, to show that (3.2) implies the global stability of $\bar{x}$. Indeed, (3.1) has the form (2.2) with $F(x) =$

$q + (1-q)e^{r(1-x)}$. It is easy to check that F satisfies (2.13). Moreover, for $g(x) = -\ln(F(e^{-x}))$, we have

$$(Sg)(x) = \frac{-1}{2} + \frac{e^{-2x}}{2}\left[\left(\frac{(1-q)re^r}{(1-q)e^r + qe^{re^{-x}}}\right)^2 - r^2\right].$$

It is clear that the expression inside the square brackets is negative for all $x \in \mathbb{R}$, and hence $(Sg)(x) < -1/2 < 0$ for all $x \in \mathbb{R}$.

An application of Corollary 2.7 gives the global stability of the positive equilibrium in (3.1) whenever $|g'(0)| \leq 2$, which is equivalent to the local stability condition (3.2).

Example 3.2. Our second example is the combination of models by Hassel and Maynard Smith (1.4). After normalization, we have equation

$$x_{n+1} = \frac{x_n(1+b)^\zeta}{\left(1 + bx_n^\xi\right)^\zeta}, \quad n = 0, 1, \ldots, \tag{3.4}$$

where $b, \xi, \zeta > 0$. This equation includes as particular cases models **VI** ($\xi = 1$) and **VII** ($\zeta = 1$) in [2, 3]. As in the previous example, (3.4) has the form (2.2); in this case,

$$F(x) = \frac{(1+b)^\zeta}{(1+bx^\xi)^\zeta}.$$

It is easy to check that F meets (2.13). On the other hand, function $g(x) = -\ln(F(e^{-x}))$ satisfies

$$g'(0) = \frac{-b\xi\zeta}{1+b} \quad ; \quad (Sg)(x) = -\frac{\xi^2}{2}\frac{1 + 2be^{-\xi x}}{(1+be^{-\xi x})^2} < 0, \forall\, x \in \mathbb{R}.$$

Hence, the local asymptotic stability condition

$$\xi\zeta \leq \frac{2(1+b)}{b} \tag{3.5}$$

implies the global stability of the positive equilibrium.

In [10], the author gets the global stability condition $\xi\zeta \leq 2$, which is the best stability condition independent of the parameter b. However, our criterion (3.5) shows that the region of the parameters for which (3.4) is globally stable is much larger when b is close to 0.

Example 3.3. Since only models **I**, **V**, **VI** and **VII** in [3] meet Assumption 1.1, and **I**, **VI** and **VII** are particular cases of our examples 3.1 and 3.2, we finish this section with a generalization of model **V**. Consider the difference equation

$$x_{n+1} = x_n\left(\frac{1+ae^b}{1+ae^{bx_n}}\right)^\xi, \quad n = 0, 1, \ldots, \tag{3.6}$$

where $a, b, \xi > 0$. Model **V** in [3] is precisely (3.6) with $\xi = 1$. In this case,

$$F(x) = \left(\frac{1+ae^b}{1+ae^{bx}}\right)^\xi,$$

and it is again easy to verify (2.13). On the other hand,

$$(Sg)(x) = -\frac{1}{2} - \frac{b^2e^{-2x}\left(1+2ae^{be^{-x}}\right)}{2\left(1+ae^{be^{-x}}\right)^2} < -\frac{1}{2} < 0, \forall\, x \in \mathbb{R}.$$

Therefore, an application of Corollary 2.7 establishes that the local asymptotic stability criterion $|g'(0)| \leq 2$ also implies the global stability of the equilibrium. This condition reads

$$ae^b(b\xi - 2) \leq 2\,.$$

4. **Final remarks.** In this note, we have established an easily verifiable criterion to show that the popular statement "L. A. S. $\Longrightarrow$ G. A. S." is true in some one-dimensional discrete-time population models in the form

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

However, as it was observed by Levin and May [4], numerical experiments suggest that this fact seems to be true also for the k-dimensional models (1.5), that is,

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

with $k \geq 1$. This population model is more appropriate when the density-dependent mechanisms operate with an explicit delay of k generations.

Assuming that F is differentiable, the boundary of the region for which the positive equilibrium $\bar{x}$ is asymptotically stable is given [4] by:

$$\bar{x}|F'(\bar{x})| = 2\cos\left(\frac{k\pi}{2k+1}\right)\,.$$

For simplicity, we assume that F is decreasing and there is a unique $\bar{x} > 0$ such that $F(\bar{x}) = 1$, which is the case in the examples considered in the previous section. Thus, analogously to the case $k = 0$, the change of variables (2.3) transforms (1.5) into

$$y_{n+1} - y_n = g(y_{n-k})\,, \quad n = 0, 1, \ldots, \tag{4.1}$$

where $g(y) = -\ln(F(\bar{x}e^{-y}))$. Recent results obtained in [7, 11] suggest the study of the following conjecture, which is the generalization of Theorem 2.3 to Equation (1.5).

Conjecture 4.1. *Assume that there exists a positive constant b_k such that*

$$r_k(y) \leq g(y) < 0\,,\ \forall\, y > 0 \quad \text{and} \quad 0 < g(y) \leq r_k(y)\,,\ \forall\, y \in (-1/b_k, 0)\,,$$

where $r_k(y) = -a_k\, y/(1 + b_k y)$, and

$$a_k = 2\cos\left(\frac{k\pi}{2k+1}\right)\,.$$

Then the equilibrium $y = 0$ is globally stable for (4.1).

We call this statement the *Levin and May conjecture.* The interested reader can find more discussions and some new related results in [7, 11]. Notice that Theorem 2.3 proves that Conjecture 4.1 is true for $k = 0$.

If the statement of Conjecture 4.1 is true, then the conclusions of Corollary 2.7 still hold for equation (1.5). This result was suggested as Conjecture 4.8 in [7]. If such a conjecture is proven, then we can extend the global stability criteria given in Section 3 to the k-dimensional versions of Examples 3.1, 3.2, and 3.3.

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E-mail address: eliz@dma.uvigo.es