



Global stability of discrete dynamical systems via exponent analysis: applications to harvesting population models

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Abstract. We present a novel approach to study the local and global stability of families of one-dimensional discrete dynamical systems, which is especially suitable for difference equations obtained as a convex combination of two topologically conjugated maps. This type of equations arise when considering the effect of harvest timing on the stability of populations.

Keywords: global stability, discrete dynamical system, population model, harvest timing.

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1 Introduction

A common problem in the study of dynamical systems is to decide whether two different systems have a *similar* behavior [12]. In some cases, solving the problem is easy. For instance, let $F_0(x) := f(rx)$ and $F_1(x) := rf(x)$, where $r \in (0, 1)$ and $f: (0, +\infty) \rightarrow (0, +\infty)$ is a continuous map. Since $F_1 = \psi \circ F_0 \circ \psi^{-1}(x)$ with $\psi(x) = rx$, the maps F_0 and F_1 are topologically conjugated and, therefore, the difference equations

$$x_{t+1} = F_0(x_t), \quad t = 0, 1, 2, \dots, \quad (1.1)$$

and

$$x_{t+1} = F_1(x_t), \quad t = 0, 1, 2, \dots, \quad (1.2)$$

are equivalent from a dynamical point of view.

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In other situations, the solution is much harder. Here, we consider a problem proposed by Cid, Liz and Hilker in [8, Conjecture 3.5]. They conjectured that if equation (1.1) has a locally asymptotically stable (L.A.S.) equilibrium, then the difference equation

$$x_{t+1} = (1 - \theta)F_0(x_t) + \theta F_1(x_t), \quad t = 0, 1, 2, \dots, \quad (1.3)$$

also has a locally asymptotically stable equilibrium for each $\theta \in [0, 1]$, provided that f is a *compensatory population* map [7]. In this paper, we show that this conjecture is true for a broad family of population maps. Indeed, for all maps in that family, we prove that the equilibrium of (1.3) is not only L.A.S. but globally asymptotically stable (G.A.S.). In other words, we provide sufficient conditions for (1.3) to inherit the global asymptotic behavior of (1.1) independently of the value of $\theta \in [0, 1]$.

Equation (1.3) arises when the effect of harvest timing on population dynamics is considered. Together with many other factors, harvest time conditions the persistence of exploited populations, especially for seasonally reproducing species [6, 19, 28, 31], which on the other hand are particularly suitable to be modeled by discrete difference equations [20]. A key question in management programmes is to ensure the sustainability of the tapped resources, thus the issue is generating an increasing interest. However, most previous studies have focused on population size and few have addressed population stability. A model proposed in [32] and based on constant effort harvesting—also known as proportional harvesting—allows for the consideration of any intervention moment during the period between two consecutive breeding seasons, a period that from now on we will call the harvesting season for the sake of simplicity. For this model, two topologically conjugated systems are obtained when the removal of individuals takes place at the beginning or at the end of the harvesting season—namely difference equations (1.1) and (1.2). For these two conjugated systems, harvesting with a certain effort—namely the value of r —can create an asymptotically stable positive equilibrium. When individuals are removed at an intermediate moment during the harvesting season, the dynamics of the population follow a convex combination of these limit cases—namely (1.3). In this framework, Conjecture 3.5 in [8] has a clear meaning with important practical consequences: delaying harvest could not destabilize populations with compensatory dynamics.

Previous works have addressed the problem considered here. Cid et al. proved in [8] that the local stability of the positive equilibrium is not affected by the time of intervention for populations governed by the Ricker model [30]. They also obtained a sharp global stability result for the quadratic map [25] and the Beverton–Holt model [5]. Global stability is always desirable as it allows to predict the fate of populations with independence of their initial size. Yet, proving it is in general a difficult task, this being reflected in the fact that many different schemes have been used in the literature for this purpose. In [14, 15], the authors showed that harvest time does not affect the global stability in the Ricker case by using well-known tools, namely results independently proved by Allwright [2] and Singer [34] for unimodal maps with negative Schwarzian derivative and a sufficient condition for global stability in [35, Corollary 9.9].

Little is known about the effect of the moment of intervention on the stability of populations governed by equations different from the Ricker model, the Beverton–Holt model or the quadratic map (although see [14, Proposition 2], where it was proved that the moment of intervention does not affect the stability when the harvesting effort is high enough). To reduce this gap, we introduce an innovative approach that is especially useful to prove the global stability of a broad family of population models, namely those encompassed in the so called

generalized α -Ricker model [24]. Among others, the Bellows, the Maynard Smith–Slatkin and the discretized version of the Richards models are covered by our analysis [4, 26, 29]. Interestingly, these three models can be seen, respectively, as generalizations of the already studied Ricker, Beverton–Holt and quadratic maps where the term related to the density dependence includes a new exponent parameter α . In the proposed new method, the focus is on α : under certain conditions, we provide sharp results of both local and global stability of the positive equilibrium of the system depending on the value of α . In particular, these results can be considered as the proof, for a wide range of population models, of [8, Conjecture 3.5]. It is important to stress that this does not prove the aforementioned conjecture in general, which is impossible since it is false [14], but supports its validity when restricted to meaningful population maps used in population dynamics.

The proposed new method can be applied whenever the per capita production function g has a strictly negative derivative. The domain $(0, \rho)$ of g can be bounded or unbounded. All bounded cases can be easily reduced to the case $\rho = 1$. The range $(g(\rho), g(0))$ can also be bounded or unbounded, provided that $0 \leq g(\rho) < 1 < g(0) \leq +\infty$.

The applications that we present in this paper focus on the cases $g(0) < +\infty$ and $g(\rho) = 0$. In particular, our examples deal with the following models:

- The *Bellows* model, which includes the *Ricker* model as a particular case (Subsection 4.1).
- The discretization of the *Richards* model, which includes the *quadratic* model as a particular case (Subsection 4.2).
- The *Maynard Smith–Slatkin* model, which includes the *Beverton–Holt* model as a particular case (Subsection 4.3).
- The *Thieme* model, which includes the *Hassell* model as a particular case (Subsection 4.4).

The paper is organized as follows. Section 2 describes the harvesting population model that motivates our study and lists the families of per capita production functions that we will consider in Section 4. Section 3 states and proves the main results. Section 4 is divided in several subsections, each of them consisting in an example of the applicability of the main results. Finally, Section 5 focuses on the “L.A.S. implies G.A.S.” and the “stability implies G.A.S” properties.

2 Model

2.1 Per capita production functions

First-order difference equations are commonly used to describe the population dynamics of species reproducing in a short period of the year. Usually, these equations take the general form

$$x_{t+1} = x_t g(x_t), \quad t = 0, 1, 2, \dots, \quad (2.1)$$

where x_t corresponds to the population size at generation t and map g to the per capita production function, which naturally has to be assumed as non-negative. In addition, g is frequently assumed to be strictly decreasing, because of the negative effect of the intraspecific competition in the population size, and when that condition holds the population is said *compensatory* [7, 20]. Theoretical ecologists have developed several concrete families of per

capita production functions. These families depend on one or several parameters, which are essential to fit the functions to the experimental data.

Our results cover some of the most relevant families of compensatory population maps, which, as it was pointed out in [24], can be described in a unified way using the map

$$g: \{x \in \mathbb{R}_{++} : 1 + px^\alpha > 0\} \rightarrow \mathbb{R}_{++}$$

defined by

$$g(x) = \lim_{q \downarrow p} \frac{\kappa}{(1 + qx^\alpha)^{1/q}}, \quad (2.2)$$

where $\alpha, \kappa \in \mathbb{R}_{++}$ and $p \in \overline{\mathbb{R}} \setminus \{-\infty\}$, with \mathbb{R}_{++} denoting the set of positive real numbers and $\overline{\mathbb{R}} := [-\infty, +\infty]$ the extended real line.

The following models are obtained for different values of the parameters:

[M1] For $p = 1$ and $\alpha = 1$, the *Beverton–Holt* model [5], in which $g(x) = \frac{\kappa}{1+x}$.

[M2] For $p = -1$ and $\alpha = 1$, the *quadratic* model [25], in which $g(x) = \kappa(1 - x)$ and where $\kappa < 4$ for (2.1) to be well-defined.

[M3] For $p = 0$ and $\alpha = 1$, the *Ricker* model [30], in which $g(x) = \kappa e^{-x}$.

Models **[M1–M3]** are compensatory. Nevertheless, **[M2–M3]** are always overcompensatory [7,9] (map $xg(x)$ is unimodal) and can have very rich and complicate dynamics, whereas **[M1]** is never overcompensatory (the map $xg(x)$ is increasing) and has pretty simple dynamics: all solutions monotonically tend to the same equilibrium which, consequently, is G.A.S.

Map (2.2) also includes models that are overcompensatory or not depending on the values of the parameters:

[M4] For $p = 1$, the *Maynard Smith–Slatkin* model [26], in which $g(x) = \frac{\kappa}{1+x^\alpha}$.

[M5] For $\alpha = 1$ and $p > 0$, the *Hassell* model [17], in which $g(x) = \frac{\kappa}{(1+px)^{1/p}}$.

[M6] For $p > 0$, the *Thieme* model [35], in which $g(x) = \frac{\kappa}{(1+px^\alpha)^{1/p}}$.

Obviously, **[M4–M6]** include **[M1]** as a special case. Similarly, the last two models that we will mention can be considered as generalizations of **[M2]** and **[M3]**, respectively:

[M7] For $p = -1$, the discretization of the *Richards* model [29], in which $g(x) = \kappa(1 - x^\alpha)$. Since $xg(x)$ attains its maximum value at $x = (1/(1 + \alpha))^{1/\alpha}$, the inequality $\alpha\kappa < (1 + \alpha)^{\frac{1+\alpha}{\alpha}}$ must be satisfied for (2.1) to be well-defined.

[M8] For $p = 0$, the *Bellows* model [4], in which $g(x) = \kappa e^{-x^\alpha}$.

Models **[M7–M8]** generalize **[M2–M3]** by including a new exponent parameter α , which determines the severity of the density dependence and makes the models more flexible to describe datasets [4]. This is the announced exponent parameter playing a central role in our study.

Before presenting the harvesting model where these population production functions will be plugged in, it is convenient to make some remarks. First, we point out that the domain of g is bounded for models **[M2]** and **[M7]**, whereas it is unbounded for the rest of models. When the domain of g is bounded, there is a restriction in the parameters involved in the

map for which (2.1) is well-defined. On the other hand, a suitable rescaling allows to obtain other frequently used expressions of these eight models depending on an extra parameter, e.g. $g(x) = \kappa(1 - mx)$ for the quadratic model or $g(x) = \kappa e^{-mx}$ for the Ricker model. This extra parameter is irrelevant for the dynamics of (2.1).

2.2 Modelling harvest timing

Assume that a population described by (2.1) is harvested at the beginning of the harvesting season t and a fraction $\gamma \in [0, 1)$ of the population is removed. Then, it is well established that the population dynamics are given by

$$x_{t+1} = (1 - \gamma)x_t g((1 - \gamma)x_t). \quad (2.3)$$

When individuals are removed at the end of the harvesting season, the population dynamics follow

$$x_{t+1} = (1 - \gamma)x_t g(x_t). \quad (2.4)$$

The above situations represent the two limit cases of our problem. To model the dynamics of populations harvested at any time during the harvesting season, we consider the framework introduced by Seno in [32]. Let $\theta \in [0, 1]$ represent a fixed time of intervention during the harvesting season, in such a way that $\theta = 0$ corresponds to removing individuals at the beginning of the season and $\theta = 1$ at the end. Assume that the reproductive success at the end of the season depends on the amount of energy accumulated during it. Given that the per capita production function depends on x_t before θ and on $(1 - \gamma)x_t$ afterwards, Seno assumed that the population production is proportional to the time period before/after harvesting. This leads to the convex combination of (2.3) and (2.4) given by

$$x_{t+1} = (1 - \gamma)x_t [\theta g(x_t) + (1 - \theta)g((1 - \gamma)x_t)]. \quad (2.5)$$

In particular, substituting $\theta = 0$ in (2.5) yields (2.3), and (2.4) is obtained for $\theta = 1$.

The two maps derived from (2.5) for $\theta = 0$ and $\theta = 1$ are topologically conjugated. Thus, if the equilibrium for $\theta = 0$ is G.A.S., then the equilibrium for $\theta = 1$ is also G.A.S., and vice versa. From a practical point of view, this implies that for these two limit cases we can predict the long-run behavior of the system with independence of the initial condition. In view of this, it is natural to study to what extent the same is true if individuals are removed at any intermediate moment during the harvesting season.

Substituting map (2.2) into (2.5), we obtain an intricate model depending on up to five parameters for which establishing general local or global stability results is a tricky task. For that purpose, we develop a general method in the following section.

3 Exponent analysis method

Consider the difference equation

$$x_{t+1} = x_t g_s(x_t),$$

with

$$g_s(x) = c h(x^\alpha) + (b - c) h(sx^\alpha),$$

where $b, s, \alpha \in \mathbb{R}_{++}$ and $c \in \mathbb{R}_+ := [0, +\infty)$ are such that $c < b$; $s \leq 1$; and $h: (0, \rho) \rightarrow (v, \mu) \subset \mathbb{R}_{++}$ is a decreasing diffeomorphism with $\rho, \mu \in \{1, +\infty\}$ and $vb < 1 < \mu b$.

Notice that the domain of h can be the open bounded interval $(0, 1)$ or the open unbounded interval $(0, +\infty)$, covering all the models described in the previous section. In addition, the image of h can be bounded or unbounded, although the applications presented in this paper are restricted to the bounded case.

For $\rho = 1$, it is not obvious that the difference equation $x_{t+1} = x_t g_s(x_t)$ is well-defined, i.e. $x g_s(x) \in (0, \rho)$ for $x \in (0, \rho)$. Next, we study when the difference equation $x_{t+1} = x_t g_s(x_t)$ is well-defined and has a unique equilibrium. We establish some notation first. Being the function

$$x \mapsto g_s \left(x^{1/\alpha} \right) = c h(x) + (b - c) h(sx)$$

a diffeomorphism from $(0, \rho)$ to $(v_s b, \mu b)$, where

$$v_s := \lim_{x \rightarrow \rho} g_s(x)/b = \frac{cv + (b - c)h(sv)}{b} \geq v, \quad (3.1)$$

we denote by j_s its inverse diffeomorphism, i.e., the function $j_s: (v_s b, \mu b) \rightarrow (0, \rho)$ satisfying

$$c h(j_s(z)) + (b - c) h(s j_s(z)) = z \quad (3.2)$$

for all $z \in (v_s b, \mu b)$. Obviously, when $\rho = +\infty$, one has $v_s = v$ for $s \in (0, 1]$.

Lemma 3.1. *Assume $b, s, \alpha \in \mathbb{R}_{++}$ and $c \in \mathbb{R}_+$ are such that $c < b$; $s \leq 1$; and $h: (0, \rho) \rightarrow (v, \mu) \subset \mathbb{R}_{++}$ is a decreasing diffeomorphism with $\rho, \mu \in \{1, +\infty\}$ and $vb < 1 < \mu b$. In addition, let*

$$s_* := \inf\{s \in (0, 1] : v_s < 1/b\}, \quad (3.3)$$

where v_s is given by (3.1). Then, the map $x g_s(x)$ has a unique fixed point in $(0, \rho)$ if and only if $s > s_*$. Moreover, this fixed point is $(j_s(1))^{1/\alpha}$.

Proof. Clearly, $x \in (0, \rho)$ is a fixed point of $x g_s(x)$ if and only if $g_s(x) = 1$, and in such case, $x = (j_s(1))^{1/\alpha}$.

Next, notice that $v_0 := \frac{cv + (b-c)\mu}{b} \geq v_{\hat{s}} \geq v_s \geq v_1 = v$, for $0 < \hat{s} < s < 1$, and that v_s depends continuously on s . Since g_s maps $(0, \rho)$ onto $(v_s b, \mu b)$ and $vb < 1 < \mu b$ holds, we have that the equation $g_s(x) = 1$, for $x \in (0, \rho)$, has solution if and only if $s > s_*$. We have already stressed that $v_s = v$, for $\rho = +\infty$. Hence, we have $s_* = 0$ for $\rho = +\infty$. \square

In the conditions of Lemma 3.1, for each $s \in (0, 1]$ we define the function

$$\tau_s: \left(\frac{1}{\mu b}, \frac{1}{v_s b} \right) \rightarrow \overline{\mathbb{R}} \quad \text{by} \quad \tau_s(z) := \frac{\ln \left(j_s \left(\frac{1}{z} \right) \right)}{\ln z}. \quad (3.4)$$

Now, we study under which conditions the difference equation $x_{t+1} = x_t g_s(x_t)$ is well-defined.

Lemma 3.2. *Assume that the conditions of Lemma 3.1 hold with $s \in (s_*, 1]$. Then, $z g_s(z) \in (0, \rho)$ for all $z \in (0, \rho)$ if and only if $\alpha < \alpha_s$ with*

$$\alpha_s = \begin{cases} +\infty, & \rho = +\infty, \\ \min_{z \in (1/\mu b, 1)} \tau_s(z), & \rho = 1. \end{cases} \quad (3.5)$$

Moreover, if the equation $x_{t+1} = x_t g_s(x_t)$ is well-defined for $s = 1$, then it is also well-defined for $s \in (s_*, 1]$.

Proof. We consider separately the cases $\rho = +\infty$ and $\rho = 1$. The case $\rho = +\infty$ is trivial. For $\rho = 1$, we have

$$z g_s(z) \in (0, 1) \text{ for } z \in (0, 1) \iff g_s(z) < \frac{1}{z} \text{ for } z \in (0, 1).$$

The latter inequality always holds if $z \leq \frac{1}{\mu b}$, because $g_s((0, 1)) = (v_s b, \mu b)$. Hence,

$$\begin{aligned} g_s(z) < \frac{1}{z} \text{ for } z \in (0, 1) &\iff g_s(z) < \frac{1}{z} \text{ for } z \in \left(\frac{1}{\mu b}, 1\right) \\ &\iff z^\alpha > j_s\left(\frac{1}{z}\right) \text{ for } z \in \left(\frac{1}{\mu b}, 1\right) \\ &\iff \alpha < \frac{\ln(j_s(\frac{1}{z}))}{\ln z} = \tau_s(z) \text{ for } z \in \left(\frac{1}{\mu b}, 1\right). \end{aligned}$$

Since $\rho = 1$, we have that $\tau_s(z) > 0$ for $z \in \left(\frac{1}{\mu b}, 1\right)$ and

$$\lim_{z \rightarrow 1/\mu b} \tau_s(z) = +\infty \quad \text{and} \quad \lim_{z \rightarrow 1^-} \tau_s(z) = +\infty, \quad (3.6)$$

which finishes the proof of the first affirmation. For the second one, notice that α_s decreases as we increase s , because j_s decreases with s . Therefore, $\alpha < \alpha_1$ guarantees $\alpha < \alpha_s$ for $s \in (s_*, 1]$. \square

Now, in the conditions of Lemma 3.1, for each $s \in (s_*, 1]$, we write

$$b_s := \min\left\{\mu b, \frac{1}{v_s b}\right\}, \quad (3.7)$$

and define the function $\sigma_s: \left(\frac{1}{b_s}, b_s\right) \subset \left(\frac{1}{\mu b}, \frac{1}{v_s b}\right) \rightarrow \mathbb{R}$ by

$$\sigma_s(z) := \begin{cases} \tau_s(z) + \tau_s\left(\frac{1}{z}\right), & z \neq 1, \\ \frac{-2j'_s(1)}{j_s(1)}, & z = 1. \end{cases} \quad (3.8)$$

Lemma 3.3. *The function σ_s given in (3.8) is continuous and positive. Moreover, when $\rho = 1$, it satisfies $\sigma_s(z) < \tau_s(z)$ for $z \in \left(\frac{1}{b_s}, 1\right)$.*

Proof. A direct application of L'Hôpital's rule shows that σ_s is a continuous function:

$$\begin{aligned} \lim_{z \rightarrow 1} \sigma_s(z) &= \lim_{z \rightarrow 1} \frac{\ln(j_s(1/z)) - \ln(j_s(z))}{\ln z} \\ &= \lim_{u \rightarrow 0} \frac{\ln(j_s(e^{-u})) - \ln(j_s(e^u))}{u} = \frac{-2j'_s(1)}{j_s(1)} = \sigma_s(1). \end{aligned}$$

On the other hand, to see that σ_s takes values on \mathbb{R}_{++} note that $z \mapsto \ln(j_s(z))$ is a decreasing function and that j_s is a diffeomorphism, so $j'_s(1) < 0$.

Finally, for $\rho = 1$, one has

$$\tau_s(z) = \frac{\ln(j_s(1/z))}{\ln z} > 0 \quad \text{and} \quad \tau_s(1/z) = \frac{\ln(j_s(z))}{-\ln z} < 0,$$

for $z \in \left(\frac{1}{b_s}, 1\right)$. Thus, $\sigma_s(z) < \tau_s(z)$ for $z \in \left(\frac{1}{b_s}, 1\right)$. \square

The function σ_s , given in (3.8), is related to the fixed points of the map $f_s \circ f_s$ with $f_s(x) = xg_s(x)$, as we will see next. Assuming $\alpha < \alpha_s$, for the map $f_s \circ f_s$ to be well-defined, and rearranging for α in the fixed points equation we have (see Lemma 3.1)

$$g_s(x)g_s(xg_s(x)) = 1 \iff j_s^{-1}(y)j_s^{-1}\left(y\left(j_s^{-1}(y)\right)^\alpha\right) = 1; y = x^\alpha \quad (3.9)$$

$$\iff zj_s^{-1}(j_s(z)z^\alpha) = 1; z = j_s^{-1}(x^\alpha) \quad (3.10)$$

$$\iff j_s(z)z^\alpha = j_s(1/z); z = j_s^{-1}(x^\alpha) \quad (3.11)$$

$$\iff \alpha = \sigma_s(z) \text{ with } z = j_s^{-1}(x^\alpha), \text{ or } z = 1. \quad (3.12)$$

In other words, the difference equation $x_{t+1} = x_tg_s(x_t)$ has a nontrivial period-2 orbit if and only if there exists $z \in (1/b_s, b_s) \setminus \{1\}$ and $\alpha < \alpha_s$ such that $\sigma_s(z) = \alpha$. Consequently, considering σ_s for the study of the global stability of the equilibrium of $x_{t+1} = x_tg_s(x_t)$ is natural since, by the main theorem in [10], the absence of nontrivial period-2 orbits for $x_{t+1} = x_tg_s(x_t)$ is equivalent to the global asymptotic stability of this equilibrium. More specifically, we will use the following result:

Lemma 3.4. *Let $-\infty \leq a_1 < a_2 \leq \infty$, $I = (a_1, a_2)$, $f : I \rightarrow I$ a continuous function and $x_\infty \in I$ such that $(f \circ f)(x) \neq x$ for all $x \in I \setminus \{x_\infty\}$. Then, x_∞ is a stable equilibrium for the map $f \circ f$ if and only if x_∞ is a G.A.S. equilibrium for the map f .*

Proof. Define $f^{(1)} := f$, $f^{(n)} := f \circ f^{(n-1)}$ and apply the Sharkovsky Forcing Theorem [33] to see that $f^{(n)}(x) \neq x$ for all $x \in I \setminus \{x_\infty\}$, $n \geq 1$. If the continuous function $q(x) = f^{(n)}(x) - x$ were negative in (a_1, x_∞) , then x_∞ would not be stable for the map $f^{(2)}$, since $x_j = f^{(2nj)}(x_0)$ would be a decreasing sequence, for all $x_0 \in (a_1, x_\infty)$. Applying the same argument for the interval (x_∞, a_2) , we conclude that $(f^{(n)}(x) - x)(x - x_\infty) < 0$ for all $n \geq 1$, $x \in I \setminus \{x_\infty\}$. In particular, replacing x with $f^{(m)}(x)$, one has $(f^{(n+m)}(x) - f^{(m)}(x))(f^{(m)}(x) - x_\infty) < 0$ for all $n, m \geq 1$, $x \in I \setminus \{x_\infty\}$. Therefore, the subsequence of $(f^{(n)}(x))_n$ formed by the terms smaller (respectively, greater) than the x_∞ is increasing (respectively, decreasing). Then, $\lim_{n \rightarrow \infty} f^{(n)}(x) = x_\infty$, for all $x \in I$. The converse is obvious. \square

Remark 3.5. We are considering per capita production functions from $(0, \rho)$ onto $(\nu_s b, \mu b) \subset (\nu b, \mu b)$, given by

$$g_s(x) = ch(x^\alpha) + (b - c)h(sx^\alpha),$$

where s and α runs, respectively, through $(s_*, 1]$ and $(0, \alpha_s)$, these being the largest intervals within which the equation $x_{t+1} = x_tg_s(x_t)$ is well-defined and has an equilibrium (see (3.1), (3.3) and (3.5)).

Probably, the most relevant applications arise for the case in which the domain is unbounded (i.e., $\rho = +\infty$). In such a particular case, $s_* = 0$, $\nu_s = \nu$ and $\alpha_s = +\infty$, for all $s \in [0, 1]$. Therefore, when $\rho = +\infty$, the equation $x_{t+1} = x_tg_s(x_t)$ is well-defined and has an equilibrium for all $s \in [0, 1]$ and $\alpha > 0$.

Moreover, we point out that the following theorem (which is the main result of this paper) can be applied under very general conditions. In particular, it holds when the per capita production function has unbounded range.

In what follows, ρ , μ , ν , b and c will be considered as constants, while s and α will be mostly seen as parameters.

Theorem 3.6. Let $\mu, \rho \in \{1, +\infty\}$, $0 < c < b$, $0 \leq vb < 1 < \mu b$ and $h: (0, \rho) \rightarrow (v, \mu)$ be a decreasing diffeomorphism. Let s_* be given by (3.1)–(3.3), α_s given by (3.4)–(3.5) and consider the families of functions $\{j_s\}_{s_*, < s \leq 1}$ and $\{\sigma_s\}_{s_*, < s \leq 1}$ defined by (3.2) and (3.8), respectively. For each $s \in (s_*, 1]$ and $\alpha \in (0, \alpha_s)$ also consider the discrete equation

$$x_{t+1} = x_t (c h(x_t^\alpha) + (b - c)h(sx_t^\alpha)), \quad x_0 \in (0, \rho). \quad (3.13)$$

(A) Then, (3.13) is well-defined, it has a unique equilibrium and

- (i) The equilibrium of (3.13) is locally asymptotically stable (L.A.S.) when $\alpha < \sigma_s(1)$ and it is unstable for $\alpha > \sigma_s(1)$.
- (ii) The equilibrium of (3.13) is globally asymptotically stable (G.A.S.) if and only if $\alpha < \sigma_s(z)$ for all $z \in (1, b_s)$ (see (3.1) and (3.7)).

(B) Additionally, assume that h satisfies

$$x \mapsto h'(x)/h'(sx) \text{ is nonincreasing for each } s \in (s_*, 1). \quad (\mathbf{H}_1)$$

If (3.13) is well-defined and its equilibrium is G.A.S. for $s = 1$, then (3.13) is well-defined and its equilibrium is G.A.S., for the same parameters, but $s \in (s_*, 1]$.

(C) Finally, assume that h satisfies

$$x \mapsto h'(x)/h'(sx) \text{ is decreasing for each } s \in (s_*, 1). \quad (\mathbf{H}_2)$$

If (3.13) is well-defined and its equilibrium is L.A.S. for $s = 1$, then (3.13) is well-defined and its equilibrium is L.A.S., for the same parameters, but $s \in (s_*, 1]$.

Proof. (A). By Lemmas 3.1 and 3.2, equation (3.13) is well-defined and has a unique equilibrium at $x_\infty = (j_s(1))^{1/\alpha}$. To prove (i), we compute the derivative at the equilibrium. Since

$$f_s(x) = x (c h(x^\alpha) + (b - c)h(sx^\alpha)) = x j_s^{-1}(x^\alpha),$$

we obtain

$$f'_s(x) = j_s^{-1}(x^\alpha) + x (j_s^{-1})'(x^\alpha) \alpha x^{\alpha-1}.$$

The evaluation of this expression at $x_\infty = (j_s(1))^{1/\alpha}$ yields

$$f'_s(x_\infty) = 1 + \alpha j_s(1) (j_s^{-1})'(j_s(1)) = 1 + \alpha \frac{j_s(1)}{j'_s(1)} = 1 - \frac{2\alpha}{\sigma_s(1)},$$

and then, since $\sigma_s(1) > 0$ holds by Lemma 3.3,

$$-1 < f'_s(x_\infty) < 1 \iff \alpha < \sigma_s(1).$$

Similarly, if $0 < \sigma_s(1) < \alpha$, then $f'_s(x_\infty) < -1$, so (3.13) is unstable.

By the symmetry of σ_s and applying an analogous argument as the one presented in (3.9)–(3.12) we obtain that

$$\sigma_s(z) \geq \alpha \quad \forall z \in (1, b_s) \iff ((f_s \circ f_s)(x) - x)(x - x_\infty) \leq 0 \quad \forall x \in (0, \rho) \setminus \{x_\infty\}. \quad (3.14)$$

To prove (ii), in view of (i) above, (3.9)–(3.12) and Lemma 3.4, just consider the following four scenarios:

- If $\alpha < \sigma_s(z)$ for all $z \in [1, b_s)$, then, by (3.14), $(f_s \circ f_s)(x) \neq x$ for all $x \in (0, \rho) \setminus \{x_\infty\}$ and x_∞ is L.A.S. Then, x_∞ is G.A.S.
- If $\alpha = \sigma_s(1) < \sigma_s(z)$ for all $z \in (1, b_s)$, then, by (3.14), $((f_s \circ f_s)(x) - x)(x - x_\infty) < 0$ for all $x \in (0, \rho) \setminus \{x_\infty\}$ and $(f_s \circ f_s)'(x_\infty) = 1$. The equilibrium x_∞ is L.A.S. for $f_s \circ f_s$. Then, x_∞ is G.A.S. for f_s .
- If $\alpha > \sigma_s(z)$ for all $z \in (1, b_s)$, then, by (3.14), $(f_s \circ f_s)(x) < x$ for all $x \in (0, x_\infty)$. Therefore, the equilibrium x_∞ is unstable.
- In any other case, the equation $x_{t+1} = f_s(x_t)$ has nonconstant periodic solutions. Therefore, the equilibrium x_∞ is not G.A.S.

(B). We start by verifying that the function $s \mapsto \sigma_s(z)$ is nonincreasing for each $z \in (1/b_s, b_s)$. Recall that v_s is nonincreasing in s (see (3.1)), so $(1/b_{\hat{s}}, b_{\hat{s}}) \subset (1/b_s, b_s)$ for any $0 < \hat{s} < s < 1$; therefore, $\sigma_s(z)$ is well-defined if $\sigma_{\hat{s}}(z)$ is. By differentiating with respect to s in

$$z = c h(j_s(z)) + (b - c) h(s j_s(z)),$$

we obtain

$$0 = c h'(j_s(z)) \frac{\partial j_s(z)}{\partial s} + (b - c) h'(s j_s(z)) \left(j_s(z) + s \frac{\partial j_s(z)}{\partial s} \right),$$

which implies

$$\frac{\partial \ln(j_s(z))}{\partial s} = \frac{\frac{\partial j_s(z)}{\partial s}}{j_s(z)} = \frac{(c - b) h'(s j_s(z))}{c h'(j_s(z)) + (b - c) s h'(s j_s(z))} = \frac{(c - b)}{c \frac{h'(j_s(z))}{h'(s j_s(z))} + (b - c)s}.$$

Since condition **(H₁)** holds and j_s is a decreasing diffeomorphism, we have that the function $z \mapsto \partial(\ln j_s(z))/\partial s$ is non-decreasing in $(1/b_s, b_s)$ for each $s \in (s_*, 1]$. Thus,

$$\frac{\partial}{\partial s} \sigma_s(z) = \frac{\partial}{\partial s} \left(\frac{\tau_s(z) + \tau_s(1/z)}{\ln z} \right) = \frac{\frac{\partial}{\partial s} \ln j_s(1/z) - \frac{\partial}{\partial s} \ln j_s(z)}{\ln z} \leq 0$$

for all $z \in (1/b_s, b_s) \setminus \{1\}$. Therefore, the function $s \mapsto \sigma_s(z)$ is nonincreasing for each $z \in (1/b_s, b_s)$.

Now, if (3.13) is well-defined for $s = 1$, by Lemma 3.2, we know that (3.13) is well-defined for $s \in (s_*, 1)$, and, if its equilibrium is G.A.S. for $s = 1$, (A)-(ii) and the fact that $\sigma_s(1/z) = \sigma_s(z)$ yield

$$\alpha < \sigma_1(z) \leq \sigma_s(z) \quad \text{for all } z \in (1/b_s, b_s) \setminus \{1\} \text{ and } s \in (s_*, 1].$$

Therefore, (3.13) is well-defined and its equilibrium is G.A.S. for all $s \in (s_*, 1]$.

(C). Following the same reasoning as in the previous case but using **(H₂)** instead of **(H₁)**, it is easy to see that the function $s \mapsto \sigma_s(z)$ is decreasing for each $z \in (1/b_s, b_s)$. As a consequence, if the equilibrium of (3.13) is L.A.S. for $s = 1$, the application of (A)-(i) yields

$$\alpha \leq \sigma_1(1) < \sigma_s(1), \quad \text{for all } s \in (s_*, 1],$$

and (3.13) is well-defined and its equilibrium is L.A.S. for all $s \in (s_*, 1]$. \square

Remark 3.7. Note that $\sigma_s \circ \exp$ is an even function, which makes it more suitable for graphical representations than σ_s itself.

Theorem 3.6 reduces the study of the local or global stability to the study of the relative position of the graph of σ_s with respect to α . Figure 3.1 illustrates this. For a fixed s , the relative position of $\min_{z \in (1, b_s)} \sigma_s(z)$, $\sigma_s(1)$ and α determines the local and global stability of the equilibrium of (3.13). Suppose that the graph of σ_s corresponds to the black curve in Figure 3.1-A. From (i) and (ii) in Theorem 3.6, we obtain that the equilibrium of (3.13) is unstable for $\alpha > \sigma_s(1)$, L.A.S. but not G.A.S. for $\min_{z \in (1, b_s)} \sigma_s(z) < \alpha < \sigma_s(1)$, and G.A.S. for $\alpha < \min_{z \in (1, b_s)} \sigma_s(z)$. Figure 3.1-B illustrates the special case when the function σ_s attains a strict global minimum at $z = 1$. In such a situation, the range of values of α for which the equilibrium is L.A.S., thanks to (i) in Theorem 3.6, is contained in the range of values of α for which it is G.A.S., thanks to (ii) in Theorem 3.6. Hence, in this case, Theorem 3.6 completely characterizes the stability of the equilibrium of (3.13): it is G.A.S. for $\alpha \leq \sigma_s(1)$ and unstable for $\alpha > \sigma_s(1)$.

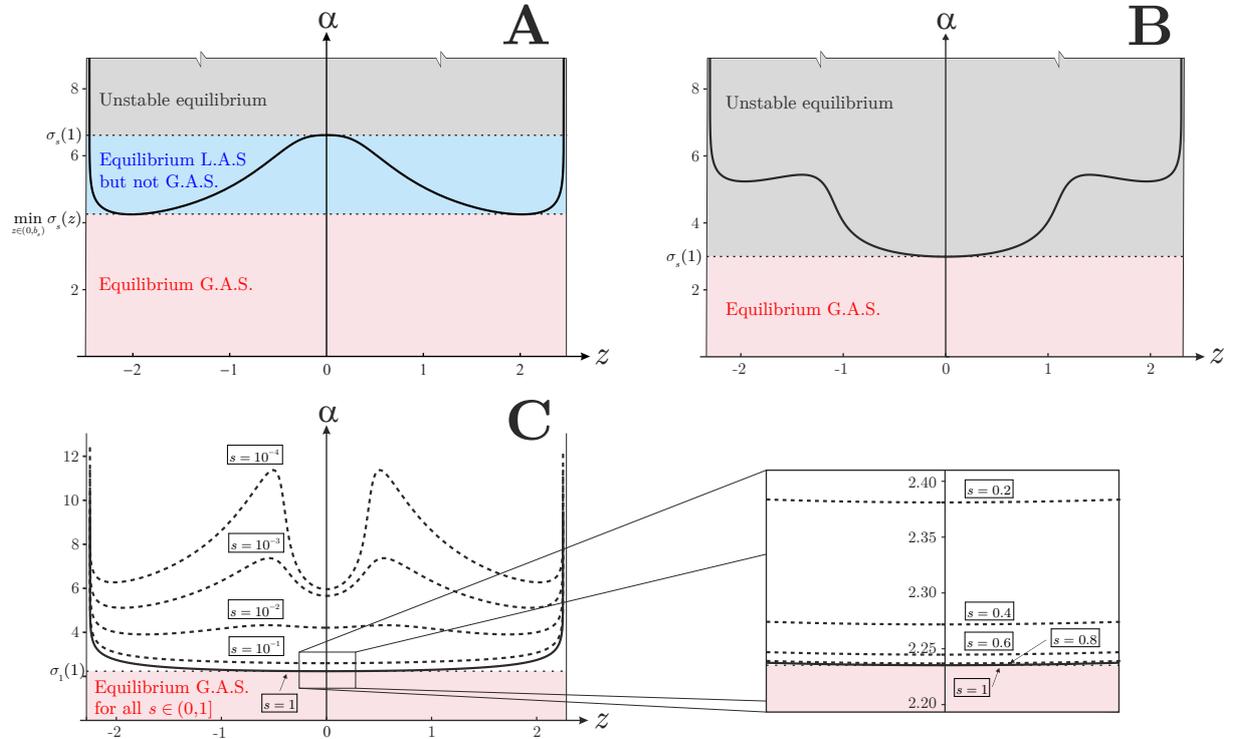


Figure 3.1: In all panels, the black curve represents the graph of $\sigma_1 \circ \exp$. **A:** For $\alpha > \sigma_s(1)$ the equilibrium of (3.13) is unstable, for $\min_{z \in (1, b_s)} \sigma_s(z) < \alpha < \sigma_s(1)$ it is L.A.S. but not G.A.S., and for $\alpha < \min_{z \in (1, b_s)} \sigma_s(z)$ it is G.A.S. **B:** Since σ_s attains at $z = 1$ a strict global minimum, the equilibrium of (3.13) is G.A.S. for $\alpha \leq \sigma_s(1)$. **C:** The assumption that σ_1 attains a strict global minimum at $z = 1$ and condition (H_1) are sufficient to guarantee that the graphs of the family of functions $\{\sigma_s\}_{0 < s \leq 1}$ are above the graph of σ_1 and, consequently, the equilibrium of (3.13) is G.A.S. for each $s \in (0, 1]$ and $\alpha \leq \sigma_1(1)$.

Figure 3.1-C deals with the last part of Theorem 3.6. Assume that $\sigma_1(1)$ is a global minimum of $\sigma_1(z)$ and that condition (H_1) holds. Then, all the graphs of the family of functions $\{\sigma_s\}_{0 < s \leq 1}$ are above the graph of $\sigma_1(z)$ and, therefore, the equilibrium of (3.13) is G.A.S. for

each $\alpha \leq \sigma_1(1)$ and $0 < s \leq 1$.

Apart from condition **(H₁)**, Theorem 3.6-(B) assumes that (3.13) is well-defined and that its equilibrium is G.A.S. for $s = 1$. But we have already mentioned that guaranteeing the G.A.S. of an equilibrium is a difficult task. Nevertheless, when the logarithmically scaled diffeomorphism $\phi_s(u) := \ln(j_s(e^u))$ is \mathcal{C}^3 , we can derive a sufficient condition for $\sigma_s(1)$ to be the strict global minimum of $\sigma_s(z)$.

Lemma 3.8. *If $\phi_s(u) := \ln(j_s(e^u))$ is three times continuously differentiable with $\phi_s'''(u) < 0$ for all $u \in (-\ln b_s, \ln b_s)$, then $\sigma_s(z)$ attains at $z = 1$ its strict global minimum value.*

Proof. It is routine to check that

$$\left[\frac{d^j (\sigma_s(e^u) u - \sigma_s(1) u)}{du^j} \right]_{u=0} = \left[\frac{d^j (\phi_s(-u) - \phi_s(u) - \sigma_s(1) u)}{du^j} \right]_{u=0} = 0$$

for $j = 0, 1, 2$, and that

$$\frac{d^3 (\sigma_s(e^u) u - \sigma_s(1) u)}{du^3} = \frac{d^3 (\phi_s(-u) - \phi_s(u) - \sigma_s(1) u)}{du^3} = -\phi_s'''(-u) - \phi_s'''(u) > 0$$

for $u \in (-\ln b_s, \ln b_s)$. Therefore, $\sigma_s(e^u) u - \sigma_s(1) u > 0$ for $u \in (0, \ln b_s)$, i.e., $\sigma_s(z) > \sigma_s(1)$ for all $z \in \left(\frac{1}{b_s}, b_s\right) \setminus \{1\}$. \square

4 Application to some population models

The next result characterizes the elements of the family of per capita production functions (2.2) for which condition **(H₁)** in Theorem 3.6 holds.

Lemma 4.1. *For any $p \in \mathbb{R}$, the function $h: \{x \in \mathbb{R}_+ : 1 + px > 0\} \rightarrow (0, 1)$ defined by*

$$h(x) = \lim_{q \downarrow p} \frac{1}{(1 + qx)^{1/q}}$$

*is a decreasing diffeomorphism. Moreover, h satisfies **(H₁)** for each $s \in (0, 1)$ if and only if $p \geq -1$.*

Proof. Assume $p \neq 0$. Differentiating, we obtain that

$$h'(x) = -(1 + px)^{-(p+1)/p} < 0$$

for any $x \in \mathbb{R}_+$ such that $1 + px > 0$ and, consequently, the first statement is true.

Moreover,

$$\frac{h'(x)}{h'(sx)} = \frac{-(1 + px)^{-(p+1)/p}}{-(1 + psx)^{-(p+1)/p}} = \left(\frac{1 + psx}{1 + px} \right)^{(p+1)/p} = \left(s + \frac{1-s}{1+px} \right)^{(p+1)/p}$$

and

$$\frac{d}{dx} \left(\frac{h'(x)}{h'(sx)} \right) = -(p+1) \left(s + \frac{1-s}{1+px} \right)^{1/p} \frac{(1-s)}{(1+px)^2},$$

which is non-positive for each $s \in (0, 1)$ if and only if $p \in [-1, +\infty) \setminus \{0\}$.

Finally, the result is straightforward for $p = 0$ since $h(x) = e^{-x}$ and $\frac{h'(x)}{h'(sx)} = e^{-(1-s)x}$. \square

The following subsections deal with the study of the harvesting model (2.5) for the per capita production functions in Subsection 2.1. We use a similar procedure for all of them, based on the following five steps:

1. First, we rewrite the difference equation that we want to study, which will depend on certain original parameters, as (3.13) with parameters $b, c, s, \alpha, \nu, \mu$ and ρ .
2. We check that h satisfies condition (H_1) , thanks to Lemma 4.1.
3. If necessary, we check that (3.13) is well-defined for $s = 1$. Next, we invoke Lemma 3.8 to guarantee that the rewritten difference equation, with $s = 1$, has an equilibrium which is G.A.S.
4. Then, we use statement (B) in Theorem 3.6 to conclude the global stability result for $s \in (s_*, 1]$.
5. Finally, we interpret the result in terms of the original parameters.

4.1 Bellows model

The per capita production function of the Bellows model is given by $g(x) = \kappa e^{-x^\alpha}$, with $\kappa, \alpha > 0$. The Seno model (2.5) is in this case

$$x_{t+1} = \kappa\theta(1 - \gamma)x_t e^{-x_t^\alpha} + \kappa(1 - \theta)(1 - \gamma)x_t e^{-(1-\gamma)^\alpha x_t^\alpha}, \quad x_0 > 0, \quad (4.1)$$

where $\theta \in [0, 1]$ and $\gamma \in [0, 1)$.

In order to apply the results in Section 3, we set $b = \kappa(1 - \gamma) > 1$, $c = \kappa(1 - \gamma)\theta$, $s = (1 - \gamma)^\alpha$, $\rho = +\infty$, $\nu = 0$, $\mu = 1$, and $h(x) = e^{-x}$, which is a decreasing diffeomorphism from $(0, +\infty)$ to $(0, 1)$ satisfying condition (H_1) , thanks to Lemma 4.1. Notice that (3.13) with $s = 1$ is equivalent to (4.1) with $\theta = 1$. In this case, $b_s = b$ for each $s \in (0, 1]$ and $j_1(z) = \ln(b/z)$ for $z \in (0, b)$, $\sigma_1(1) = 2/\ln b$. Moreover, $\phi_1(u) = \ln(\ln(b e^{-u}))$ and $\phi_1'''(u) = -\frac{2}{(\ln(b e^{-u}))^3} < 0$ for $u \in (-\ln b, \ln b)$.

Therefore, a direct application of Theorem 3.6, taking into account that $s_* = 0$, $\nu_s = \nu$ and $\alpha_s = +\infty$, for all $s \in [0, 1]$ when $\rho = +\infty$ (see Remark 3.5), yields the following result:

Proposition 4.2. *If $\kappa(1 - \gamma) > 1$, then (4.1) has a unique equilibrium. If, in addition, $\theta = 1$, then the equilibrium of (4.1) at $x = (\ln(\kappa(1 - \gamma)))^{1/\alpha}$ is unstable for $\alpha > 2/\ln(\kappa(1 - \gamma))$ and G.A.S. for $\alpha \leq 2/\ln(\kappa(1 - \gamma))$. Furthermore, for $\theta < 1$ and $\alpha \leq 2/\ln(\kappa(1 - \gamma))$, the equilibrium is also G.A.S.*

Proposition 4.2 characterizes the global stability of the equilibrium for the Bellows model without harvesting. Such a result is new, as far as we know, and is interesting in itself. On the other hand, Proposition 4.2 confirms that, for the Bellows model, the harvesting effort necessary for stabilization is less for $\theta \in (0, 1)$ than for $\theta = 0$ and $\theta = 1$. Since the Bellows model has the Ricker model as a particular case, Proposition 4.2 generalizes [8, Proposition 3.3] and gives an alternative proof of the main result in [15].

4.2 Discretization of the Richards model

The per capita production function of the discretization of the Richards model is given by $g(x) = \kappa(1 - x^\alpha)$, with $\kappa, \alpha > 0$. Hence, the Seno model (2.5) reads

$$x_{t+1} = \kappa\theta(1 - \gamma)x_t(1 - x_t^\alpha) + \kappa(1 - \theta)(1 - \gamma)x_t(1 - (1 - \gamma)^\alpha x_t^\alpha), \quad x_0 \in (0, 1), \quad (4.2)$$

where $\theta \in [0, 1]$ and $\gamma \in [0, 1)$.

In this example, it is natural to assume that (4.2) is well-defined for $\gamma = 0$, i.e., that the population model without harvesting makes sense. As mentioned when we presented this per capita production function in Subsection 2.1, equation (4.2) is well-defined for $\gamma = 0$ if and only if $\alpha\kappa < (1 + \alpha)^{\frac{1+\alpha}{\alpha}}$.

As in the previous case, we set $b = \kappa(1 - \gamma) > 1$, $c = \kappa(1 - \gamma)\theta$, $s = (1 - \gamma)^\alpha$, $\rho = 1$, $\nu = 0$, $\mu = 1$, and $h(x) = 1 - x$. Clearly, the function $h(x)$ is a decreasing diffeomorphism from $(0, 1)$ to $(0, 1)$ and, by Lemma 4.1, satisfies condition (\mathbf{H}_1) .

We aim to obtain a global stability result for (3.13) with $s = 1$, which is equivalent to (4.2) with $\theta = 1$. Note that (3.13) is well-defined for $s = 1$ because $\alpha b \leq \alpha\kappa < (1 + \alpha)^{\frac{1+\alpha}{\alpha}}$. We have $j_1(z) = 1 - \frac{z}{b}$ for $z \in (0, b)$, being $\sigma_1(1) = \frac{2}{b-1}$, $\phi_1(u) = \ln(1 - \frac{e^u}{b})$ and $\phi_1'''(u) = -\frac{be^u(b+e^u)}{(b-e^u)^3} < 0$. Then, $\sigma_1(z) > \frac{2b}{b-1}$ for $z > 1$ and the equilibrium of (3.13) is G.A.S. for $s = 1$ if $\alpha \leq \frac{2b}{b-1}$, i.e., if $b(\alpha - 2) \leq \alpha$.

In order to use Theorem 3.6, we need to impose $s > s_* = \max\{0, 1 - \frac{1}{b-c}\}$, or what is the same, $\nu_s b = (b - c)(1 - s) < 1$. But, for the selected values of the parameters, this is always true because

$$(b - c)(1 - s) = (1 - \theta)\kappa(1 - \gamma)(1 - (1 - \gamma)^\alpha) \leq \kappa(1 - \gamma)(1 - (1 - \gamma)^\alpha) < 1,$$

where we have used that $x_{t+1} = \kappa x_t(1 - x_t^\alpha)$, $x_0 \in (0, 1)$ is well-defined.

Proposition 4.3. *If $\kappa(1 - \gamma) > 1$ and $\alpha\kappa < (1 + \alpha)^{\frac{1+\alpha}{\alpha}}$, then (4.2) is well-defined and has a unique equilibrium. If, in addition, $\theta = 1$, then the equilibrium of (4.2) is unstable for $\kappa(1 - \gamma)(\alpha - 2) > \alpha$ and G.A.S. for $\kappa(1 - \gamma)(\alpha - 2) \leq \alpha$. Furthermore, for $\theta < 1$ and $\kappa(1 - \gamma)(\alpha - 2) \leq \alpha$, the equilibrium of (4.2) is also G.A.S.*

To our knowledge, Proposition 4.3 gives the first global stability result for the discretization of the Richards model even in the case without harvesting. Notice that the results in [22] cannot be used in this case since $\rho \neq +\infty$. In the harvesting framework, Proposition 4.3 includes [8, Proposition 3.6] as a particular result, where the quadratic model was considered.

4.3 Maynard Smith–Slatkin model

If we focus on populations governed by the Maynard Smith–Slatkin model, the per capita production function is given by $g(x) = \frac{\kappa}{1 + x^\alpha}$, where $\kappa > 0$ and $\alpha > 0$. In that case, model (2.5) is

$$x_{t+1} = \kappa\theta(1 - \gamma)\frac{x_t}{1 + x_t^\alpha} + \kappa(1 - \theta)(1 - \gamma)\frac{x_t}{1 + (1 - \gamma)^\alpha x_t^\alpha}, \quad x_0 > 0, \quad (4.3)$$

where $\theta \in [0, 1]$ and $\gamma \in [0, 1)$.

In [8], following [1, Appendix S1] and [23, Theorem 1], it was stated that the equilibrium of (4.3) for $\theta = 0$ is G.A.S. if $1 < \kappa(1 - \gamma) \leq \frac{\alpha}{\alpha - 2}$. No result is known about global dynamics of (4.3), in the general case. However, this model can be easily handled thanks to Theorem 3.6 and Lemma 4.1.

Consider (3.13) with $b = \kappa(1 - \gamma) > 1$, $c = \kappa(1 - \gamma)\theta$, $s = (1 - \gamma)^\alpha$, $\rho = +\infty$, $\nu = 0$, $\mu = 1$ and $h(x) = 1/(1 + x)$, which satisfies condition (\mathbf{H}_1) from Lemma 4.1. Then, $j_1(x) = \frac{b}{x} - 1$, $\sigma_1(1) = \frac{2b}{b-1}$, $\phi_1(u) = \ln(be^{-u} - 1)$, and $\phi_1'''(u) = -\frac{be^u(b+e^u)}{(b-e^u)^3} < 0$.

Now, observe again that (3.13) with $s = 1$ corresponds to (4.3) with $\theta = 1$, and apply Theorem 3.6, taking into account that $s_* = 0, v_s = v$ and $\alpha_s = +\infty$, for all $s \in [0, 1]$ when $\rho = +\infty$ (see Remark 3.5).

Proposition 4.4. *If $\kappa(1 - \gamma) > 1$, then (4.3) has a unique equilibrium. If, in addition, $\theta = 1$, then the equilibrium of (4.3) is unstable for $\kappa(1 - \gamma)(\alpha - 2) > \alpha$ and G.A.S. for $\kappa(1 - \gamma)(\alpha - 2) \leq \alpha$. Furthermore, for $\theta < 1$ and $\kappa(1 - \gamma)(\alpha - 2) \leq \alpha$, the equilibrium is also G.A.S.*

It is interesting to note that considering the exponent parameter α in the quadratic model, i.e., studying the discretization of the Richards model, unveils the complete parallelism between the Maynard Smith–Slatkin model and the quadratic model with respect to stability results.

4.4 Hassell and Thieme models

As already mentioned, topologically conjugated production functions give rise to equivalent dynamical behaviors. However, when a convex combination of the type of (2.5) is applied to two topologically conjugated production functions, the transformed systems could exhibit different dynamical behaviors.

When applying Theorem 3.6, while working in the case $s = 1$, we can replace our production function by a topologically conjugated one, for which calculations are simpler. This replacement is no longer valid when checking condition (H_1) .

In this subsection, we put into practice the previous approach to study the two models still left: Thieme's and Hassell's models. Since Thieme's model has Hassell's model as a particular case, we only consider the former. Besides, without loss of generality, we assume the per capita production function of the Thieme model to be given by

$$g(x) = \frac{\kappa}{(1 + x^\alpha)^\beta}, \quad \kappa, \alpha, \beta > 0.$$

Now, the change of variables $y_t = x_t^{1/\beta}$ shows that the dynamics of the difference equation

$$x_{t+1} = \frac{\kappa x_t}{(1 + x_t^\alpha)^\beta} \tag{4.4}$$

are identical of those of the equation

$$y_{t+1} = \frac{\kappa^{1/\beta} y_t}{1 + y_t^{\alpha\beta}},$$

whose per capita production function, $g(x) = \frac{\kappa^{1/\beta}}{1 + x^{\alpha\beta}}$, belongs to the Maynard Smith–Slatkin family of maps. This provides a straightforward way to characterize the global stability of the Thieme model.

Proposition 4.5. *If $\kappa > 1$, then (4.4) has a unique equilibrium. In addition, the equilibrium of (4.4) is unstable for $\kappa^{1/\beta}(\alpha\beta - 2) > \alpha\beta$ and G.A.S. for $\kappa^{1/\beta}(\alpha\beta - 2) \leq \alpha\beta$.*

The previous result improves the global stability condition presented in [35] with a simpler proof than the one used in [22], which relies in calculating the sign of a certain Schwarzian derivative.

The Seno model (2.5) for the Thieme production function is

$$x_{t+1} = \frac{\kappa\theta(1-\gamma)x_t}{(1+x_t^\alpha)^\beta} + \frac{\kappa(1-\theta)(1-\gamma)x_t}{(1+(1-\gamma)^\alpha x_t^\alpha)^\beta}. \quad (4.5)$$

Again, in order to apply the results in Section 3, we set $b = \kappa(1-\gamma) > 1$, $c = \kappa(1-\gamma)\theta$ and $h(x) = \frac{1}{(1+x)^\beta}$, which is a decreasing diffeomorphism from $(0, +\infty)$ to $(0, 1)$ satisfying condition (\mathbf{H}_1) , thanks to Lemma 4.1. And we get the following new result about the Thieme model under harvesting.

Proposition 4.6. *If $\kappa(1-\gamma) > 1$, then (4.5) has a unique equilibrium. If, in addition, $\theta = 1$, then the equilibrium of (4.5) is unstable for $[\kappa(1-\gamma)]^{1/\beta}(\alpha\beta-2) > \alpha\beta$ and G.A.S. for $[\kappa(1-\gamma)]^{1/\beta}(\alpha\beta-2) \leq \alpha\beta$. Furthermore, for $\theta < 1$ and $[\kappa(1-\gamma)]^{1/\beta}(\alpha\beta-2) \leq \alpha\beta$, the equilibrium is also G.A.S.*

Altogether, we have shown that [8, Conjecture 3.5] holds when restricted to the per capita production functions **[M1–M8]**. Indeed, we have shown that a stronger result holds since we are able to guarantee that the equilibrium is G.A.S. for $\theta \in (0, 1)$. Furthermore, using part C of Theorem 3.6 we obtain the following general local stability result in the spirit of [8, Conjecture 3.5].

Corollary 4.7. *Assume that $g: (0, +\infty) \rightarrow (0, +\infty)$ satisfies (\mathbf{H}_2) ; $g'(x) < 0$ for all $x > 0$; $g(0^+) > 1$; and there exists some $d > 0$ such that $xg(x)$ is strictly increasing on $(0, d)$ and strictly decreasing on $(d, +\infty)$. Then, if the equilibrium (2.5) with $\theta = 0$ is L.A.S., then the equilibrium of (2.5) is L.A.S. for all $\theta \in [0, 1]$.*

5 On the “L.A.S. implies G.A.S.” property

Global stability is a desirable property of systems as it allows to predict the fate of orbits with independence of the initial condition. For many well-known discrete population models, the local asymptotic stability of the equilibrium implies its global asymptotic stability; e.g., see [3, 11, 13, 16, 21, 22, 27]. However, determining whether this popular statement in population dynamics is true when delayed harvesting is exerted on populations governed by any of the well-known models **[M3–M8]** is an open problem. Although the property “L.A.S. implies G.A.S.” has been cited many times, we have not been able to find a definition of it in the literature, so we provide the following here.

Definition 5.1. Let \mathfrak{F}_0 be a set of maps $f: U_f \subset \mathbb{R}_+ \rightarrow U_f$, each of them having a unique fixed point $x_f \in U_f$. Given $\mathfrak{F} \subset \mathfrak{F}_0$, we say that the family of discrete equations

$$x_{t+1} = f(x_t), \quad x_0 \in U_f,$$

with $f \in \mathfrak{F}$ (or \mathfrak{F} itself) satisfies the “L.A.S. implies G.A.S.” property when

$$\{f \in \mathfrak{F} : x_f \text{ is L.A.S.}\} = \{f \in \mathfrak{F} : x_f \text{ is G.A.S.}\}.$$

Analogously, we say that \mathfrak{F} satisfies the “stability implies G.A.S.” property when

$$\{f \in \mathfrak{F} : x_f \text{ is stable}\} = \{f \in \mathfrak{F} : x_f \text{ is G.A.S.}\}.$$

Note that both properties are inherited by subsets. It should also be stressed that a family \mathfrak{F} trivially satisfies both properties when x_f is G.A.S. for all $f \in \mathfrak{F}$. Moreover, these properties lack interests when \mathfrak{F} is a singleton, $\mathfrak{F} = \{f\}$. We will avoid affirming that such families satisfy these properties in that case.

A direct application of our main theorem leads to the following results about the “stability implies G.A.S.” and “L.A.S. implies G.A.S.” properties.

Let \mathfrak{F}_0 be the set of functions $f: (0, \rho) \rightarrow (0, \rho)$ for which there exist $\mu, \rho \in \{1, +\infty\}$, $0 < c < b$, $v \geq 0$, $0 \leq s \leq 1$ and a decreasing diffeomorphism $h: (0, \rho) \rightarrow (v, \mu)$ such that $0 \leq cv + (b - c)h(s\rho) < 1 < \mu b$ and $f(x) = x(ch(x) + (b - c)h(sx))$.

For each $\mathfrak{F} \subset \mathfrak{F}_0$ denote by $\widehat{\mathfrak{F}}$ the family of functions $f(x) = xg(x^\alpha)$ where g runs through all functions satisfying $xg(x) \in \mathfrak{F}$ and α runs through all positive real numbers for which $xg(x^\alpha) \in \mathfrak{F}_0$.

Corollary 5.2. *Let $\mathfrak{F} \subset \mathfrak{F}_0$. The family $\widehat{\mathfrak{F}}$ satisfies the “stability implies G.A.S.” property if and only if the map $\sigma_s(z)$ attains its strict global minimum at $z = 1$, for each function in \mathfrak{F} .*

Proof. Suppose that there exists a function in \mathfrak{F} for which the corresponding map σ_s satisfies $\sigma_s(z_0) \leq \sigma_s(1)$ for some $z_0 \neq 1$ in $\text{dom } \sigma_s$. On the one hand, if $\sigma_s(z_0) < \sigma_s(1)$, by considering $\alpha \in (\sigma_s(z_0), \sigma_s(1))$, we find a case for which the equilibrium x_∞ is L.A.S., but not G.A.S. (apply part (A) in Theorem 3.6). On the other hand, if $\sigma_s(z) \geq \sigma_s(1)$ for all $z \in \text{dom } \sigma_s$, we consider $\alpha = \sigma_s(1)$. In this case (see (3.14)), we would have $f'_s(x_\infty) = -1$ and $((f_s \circ f_s)(x) - x_\infty)(x - x_\infty) \leq 0$ for all $x \in (0, \rho)$, and thus the equilibrium x_∞ is stable. However, this equilibrium is not G.A.S., because $\alpha = \sigma_s(z_0)$ (apply part (A) in Theorem 3.6 again). In both cases, the above family of discrete equations does not satisfy the “stability implies G.A.S.” property.

Conversely, assume that there is a function in \mathfrak{F} and an admissible value of $\alpha > 0$ for which the corresponding equilibrium x_∞ is stable, but not G.A.S. By part (A) in Theorem 3.6, $\alpha \leq \sigma_s(1)$ and there exists $z_0 \in \text{dom } \sigma_s$ with $\alpha = \sigma_s(z_0)$. In this case, the map $\sigma_s(z)$ does not attain its strict global minimum at $z = 1$. \square

We consider now \mathfrak{F}_1 to be the set of those functions $f \in \mathfrak{F}_0$ for which $s = 1$ and h satisfies condition **(H₁)** and \mathfrak{F}_2 to be the set of those functions $f \in \mathfrak{F}_0$ for which $\alpha \leq \sigma_1(1)$ and h satisfies condition **(H₁)**.

Corollary 5.3. *Let $\mathfrak{F} \subset \mathfrak{F}_0$ be such that $\widehat{\mathfrak{F}} \cap \mathfrak{F}_1$ satisfies the “L.A.S. implies G.A.S.” property. Then, x_f is G.A.S. for every function $f \in \widehat{\mathfrak{F}} \cap \mathfrak{F}_2$.*

The above statement can be reformulated as follows.

*Assume that h satisfies **(H₁)**. If (3.13) satisfies the “L.A.S. implies G.A.S.” property for $s = 1$, then, (3.13) is well-defined and its equilibrium is G.A.S. for $s \in (s_*, 1]$ and $\alpha \in (0, \sigma_1(1))$.*

Proof. Apply the part (B) in Theorem 3.6 and Corollary 5.2. \square

Observe that Corollary 5.3 does not mean that (3.13) satisfies the “L.A.S. implies G.A.S.” property for $s \in (s_*, 1]$, $\alpha \in (0, \alpha_s)$, and h satisfying condition **(H₁)**.

Finally, consider the set $\mathfrak{F}_3 \subset \mathfrak{F}_0$ made up of those functions for which the logarithmically scaled diffeomorphism $\phi_s(u) := \ln(j_s(e^u))$ is \mathcal{C}^3 with negative third derivative.

Corollary 5.4. *The family \mathfrak{F}_3 satisfies the “stability implies G.A.S.” property.*

The above statement can be reformulated as follows.

If $\phi_s(u) := \ln(j_s(e^u))$ is three times continuously differentiable with $\phi_s'''(u) < 0$ for all $u \in (-\ln b_s, \ln b_s)$, then (3.13) satisfies the “stability implies G.A.S.” property.

Proof. Apply Lemma 3.8 and Corollary 5.2. □

Remark 5.5. Corollary 2.7 in [22] is a consequence of Corollary 5.4 above for $s = 1$ and $\rho = +\infty$. Indeed, function g in [22] corresponds to

$$g(y) = -\ln(bh(e^{-\alpha y})) = -\phi_1^{-1}(-\alpha y) - \ln b,$$

up to normalization. Therefore,

$$Sg < 0 \implies S\phi_1 > 0 \implies \frac{\phi_1'''}{\phi_1'} > 0 \implies \phi_1''' < 0,$$

where S denotes the Schwarzian derivative: $(Sg)(z) := \frac{g'''(z)}{g'(z)} - \frac{3}{2} \left(\frac{g''(z)}{g'(z)} \right)^2$.

5.1 L.A.S. does not imply G.A.S. for Seno's model

In Section 4, it was proved that for models [M1–M8] the property “L.A.S implies G.A.S.” is true for $\theta \in \{0, 1\}$. In view of this, it would be natural to conjecture the validity of the property for (2.5) with any intervention moment $\theta \in [0, 1]$. Nevertheless, the conjecture would be false. To prove this, under the conditions of Theorem 3.6, it is enough to find population parameters for which $\min_{z \in (1, b)} \sigma_s(z) < \sigma_s(1)$. Surprisingly, the counterexample can be found using one of the models for which we have seen that harvest time is not destabilizing, namely the Maynard Smith–Slatkin model. Consider (3.13) for $h(x) = 1/(1+x)$, $b = 10.35$, $c = 9.16286$ and $s = 0.000150618$. The global minimum of σ_s is in that case approximately 5.77, while $\sigma_s(1) \approx 11.80$. Hence, according to Theorem 3.6, the equilibrium is L.A.S. but not G.A.S. for any $\alpha \in (5.77, 11.80)$ (cf., Figure 5.1-A).

If we fix $\alpha = 5.9$, the aforementioned equation is equivalent to (4.3) for $\kappa = 46$, $\gamma = 0.775$ and $\theta = 0.8853$. From the biological point of view, the latter corresponds to a certain population that is harvested at a given moment during the harvesting season. Let us study the effect that changing the moment of intervention would have on the stability of the equilibrium size of this population. If harvesting was exerted at the beginning or at the end of the season (i.e., $\theta = 0$ or $\theta = 1$), the equilibrium would be unstable (the derivative of the production function at that point is approximately -4.33). The above discussion shows that harvest timing can be stabilizing by itself in this case, since we have seen that the equilibrium is L.A.S. for $\theta \approx 0.8853$. Numerical simulations reveal that this happens not only for this intervention moment but for all those ranging from 0.8546 to 0.9368, approximately. However, the asymptotic stability of the equilibrium is only local for all these harvest times, given that the inequality $\min_{z \in (1, b_s)} \sigma_s(z) \leq \alpha < \sigma_s(1)$ holds for all of them.

The local stability of the equilibrium implies that nearby orbits are attracted towards it, being the convergence speed determined by the absolute value of the derivative of the production function at that point. In the case considered above, harvest time is not only stabilizing but can also turn the equilibrium into superstable by reducing that derivative to zero. This happens for two intervention moments, namely $\theta \approx 0.8853$ and $\theta \approx 0.918668$ (cf., Figure 5.1-B). On the other hand, we have seen that for $\theta \approx 0.8853$ the equilibrium is not G.A.S., and thus some nonzero orbits escape from its attraction. It would be possible that this only happened for few initial conditions, but it is not the case and the equilibrium coexists with another positive attractor, namely an attracting 12-cycle (cf., Figure 5.1-C).

This example shows that the stabilization of a population through a delay in the time of intervention is a sensitive issue: we could achieve the local stability of the equilibrium,

even with the fastest possible convergence of nearby orbits and, at the same time, induce bistability in the global population dynamics. Such a situation is in general undesirable, since small perturbations could lead to sudden sharp changes in the population size. Finally, this example provides a family of first order difference equations arising in population dynamics where “L.A.S. does not imply G.A.S.”. We note that for higher order difference equations motivated by population dynamics, it was showed recently in [18] that “L.A.S. does not imply G.A.S.” for Clark’s equation with a nonlinearity with negative Schwarzian derivative if the order of the equation is at least four.

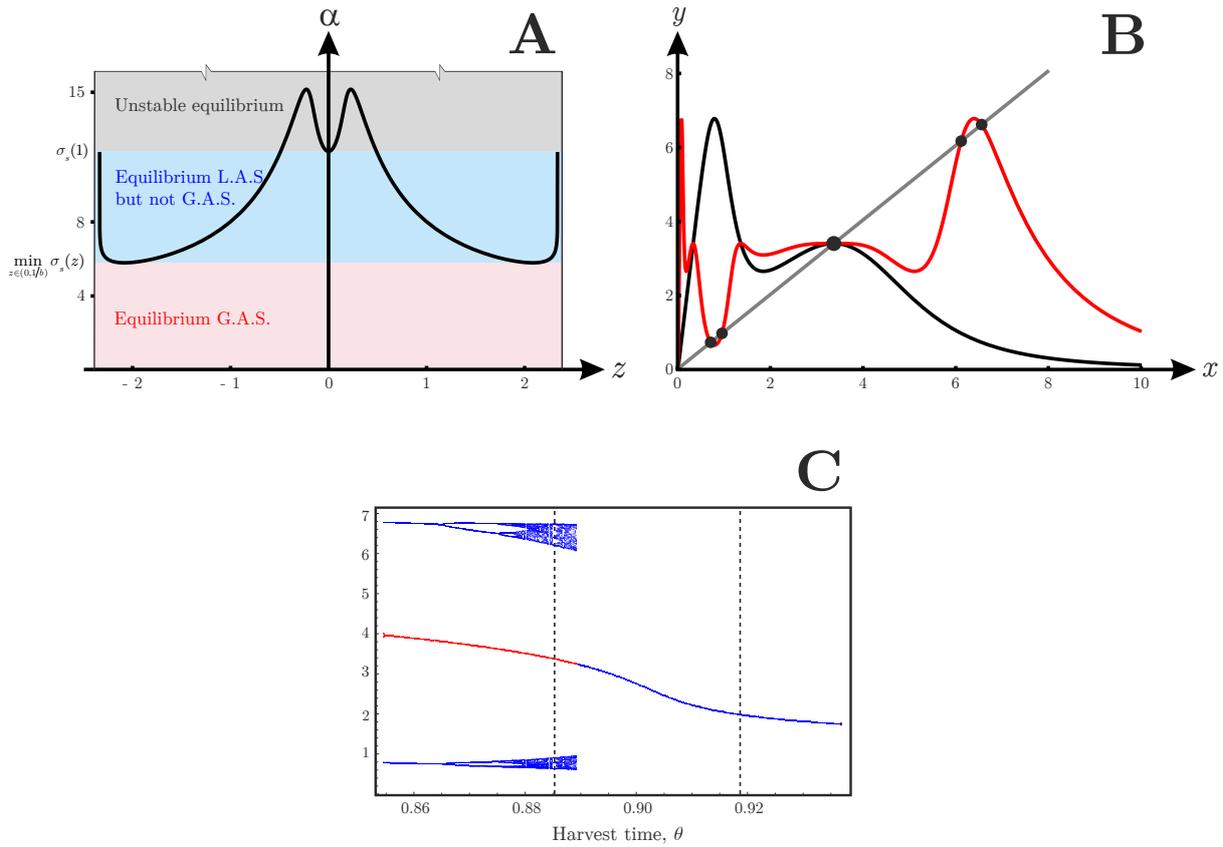


Figure 5.1: A: The black curve corresponds to $\sigma_s \circ \exp$ for (3.13) with $h(x) = 1/(1+x)$, $b = 10.35$, $c = 9.16286$ and $s = 0.000150618$. For $\alpha < \min_{z \in (1,b)} \sigma_s(z)$ the equilibrium is G.A.S., for $\min_{z \in (1,b)} \sigma_s(z) < \alpha < \sigma_s(1)$ it is L.A.S. but not G.A.S., and for $\alpha > \sigma_s(1)$ it is unstable. B: The black curve corresponds to the production function f given by (4.3) for $\kappa = 46$, $\alpha = 5.9$, $\gamma = 0.775$ and $\theta = 0.8853$, and the red curve corresponds to $f \circ f$. C: Bifurcation diagram of (4.3) for $\kappa = 46$, $\alpha = 5.9$, $\gamma = 0.775$ for varying harvest time in the range for which the equilibrium is locally asymptotically stable. Red dots correspond to the initial condition $x_0 = 6$, and blue dots correspond to $x_0 = 6.6$. The vertical dashed lines represent the intervention moments for which the equilibrium is superstable (namely $\theta \approx 0.8853$ and $\theta \approx 0.918668$).

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