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ORIGINAL ARTICLE

Population Models: Stability in One Dimension[1]

Paul Cull*

Computer Science Deptartment, Oregon State University, Corvallis, OR 97331, USA

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Abstract Some of the simplest models of population growth are one dimensional nonlinear difference equations. While such models can display wild behavior including chaos, the standard biological models have the interesting property that they display global stability if they display local stability. Various researchers have sought a simple explanation for this agreement of local and global stability. Here, we show that *enveloping* by a linear fractional function is sufficient for global stability. We also show that for seven standard biological models local stability implies enveloping and hence global stability. We derive two methods to demonstrate enveloping and show that these methods can easily be applied to the seven example models.

Although enveloping by a linear fractional is a sufficient for global stability, we show by example that such enveloping is not necessary. We extend our results by showing that *enveloping implies global stability* even when $f(x)$ is a discontinuous multi-function which might be a more reasonable description of real bilogical data. We show that our techniques can be applied to situations which are not population models. Finally, we give examples of population models which have local stability but not global stability.

Keywords Population models · Growth models · Stability · Local stability · Global stability · Linear fractional functions · Difference equations · Recurrences · Maps of the interval · Chaos

1. Introduction

Simple population growth models have a pleasant property, they display global convergence if they have local convergence. This fact was established for a number of models by Fisher et al. (1979) and Goh (1979) who constructed an explicit Lyapunov function for each model they studied. Since then a number of workers have created a variety of sufficient conditions to demonstrate global stability.

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*Corresponding author.
E-mail address: pc@cs.orst.edu (P. Cull).

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(Singer, 1978; Rosenkranz, 1983; Cull, 1981, 1986, 1988a,b) Each of these methods suffer from the difficulty that either the method does not apply to one of the commonly used models or the method is computationally difficult to apply.

In this paper, we describe a simple condition which is satisfied by all the commonly used simple population models, and we show that for these models the computation for the method is not difficult. Our simple condition is that the population models are *enveloped* by *linear fractional functions*. No single linear fractional serves for all models. Instead the linear fractionals depend on a single parameter which must be adjusted for the particular model. In some cases, this parameter will also change depending on the parameters of the model. This parameter dependence may be why this simple condition has not been discovered before.

Our pleasure with this result is not solely mathematical. There is also a psychological component. We suspect that the original creators of these models were good biologists and not sophisticated mathematicians. If the similarity among these models required deep and complicated mathematics, we would feel that we had not captured the simple vision of the original modelers. We will argue that the usual way of writing these models suggests an implicit constraint that will force enveloping by a linear fractional.

Further, we also mention a result noted by Singer (1978) and Cull (1988b) that the usual models are *buffered*, that is, making the model slightly more complicated will *not* change the local stability implies global stability result. On the other hand, we mention that it is trivial for a mathematician to create more complicated models in which either the enveloping or the local implies global result do not hold.

2. Simple population models

The simplest difference equation model for population growth is

$$x_{t+1} = r x_t,$$

where x_t is a measure of the population size at time t, and r is a growth rate. Much of biological reality has been stripped from this model. For example, individuals, sexes, ages, and spatial distribution have all been ignored. On the other hand, this simple model may make useful predictions in certain circumstances. For example, when a new species is introduced into or invades a favorable environment, the growth of the introduced species may initially follow this simple model. For longer range predictions this model is untenable, since it predicts that

$$x_t = r^t x_0,$$

and such exponential growth cannot be sustained. (Although there is some question about whether the human population is still showing exponential growth.)

More reasonable models assume that the growth rate decreases with the population size. For example, the quadratic model

$$x_{t+1} = x_t[1 + (r - 1)(1 - x_t/K)]$$

is often used. Here the growth rate is r when x is small, and if x reaches K, then the rate becomes 1 and one may hope that the population size will stay at K. One might guess that regardless of the initial population size, this model would predict that the population size would eventually approach K. This guess can be supported by the observation that this discrete time model is analogous to the differential equation

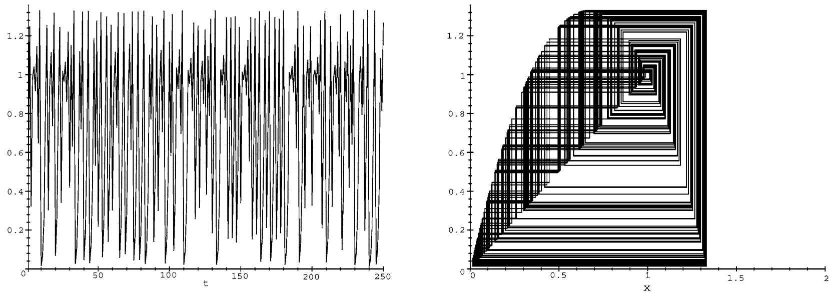
$$\frac{\mathrm{d}x}{\mathrm{d}t} = x(r-1)(1-x/K),$$

and it can obviously be argued that as long as $r > 1$ and the initial population size $x(0)$ is positive then $\lim_{t\to\infty} x(t) = K$. This convergence follows because $x(t)$ is restricted to smooth evolution on the line. So $x(t)$ cannot jump and, in particular, $x(t)$ cannot jump over K. Here if $x(0) < K$ then $x(t)$ is monotonically increasing toward K, while if $x(0) > K$ then $x(t)$ is monotonically decreasing toward K.

But things are not so simple when one considers the difference equation rather than the differential equation. At least from the time of Euler, it has been known that one must choose the step size small enough for the difference equation to behave like the differential equation. In particular, as x approaches K, one must make the step size small enough to prevent x from jumping over K. This choice of step size would result in a rescaled smaller r being used in the difference equation. Clearly, this rescaling is simply an inconvenience if one is considering the differential equation as the real model and the difference equation as merely a computational approximation to the real model. But, if one accepts the difference equation as the real model, then jumping over K is a phenomenon which cannot be ignored. Luckily, in this example, if r is small, nothing too dreadful happens. The solution to the difference equation jumps back and forth over K, but in the long run the solution approaches K, as one would have predicted from the differential equation. Convergence is not lost, but monotonicity is lost.

This description of the relation between differential and difference equations would have been satisfactory to most modelers 30 years ago, but things changed in the 70's. In particular, May's (1974, 1976) examples demonstrated that difference equations had more complicated behavior than differential equations. Instead of simple convergence, difference equations displayed wild cycles and a phenomenon which Li and Yorke (1975) called *chaos*. Figure 1(a) shows the time trajectory of a difference equation in the chaotic regime. Figure 1(b) shows a phase portrait of this trajectory. This paper will not focus on chaos. We refer the interested reader to the introductory text by Devaney (1986). Dubois has used similar difference equations to explain incursion and hyperincursion. We will not treat these issues here. We refer the interested reader to Dubois' paper (Dubois, 1998) and the references cited there. We will study the simpler issue of convergence behavior in difference equation models.

Since the differential equation models converge to K regardless of the starting point, we will call such a model *globally stable*. For difference equations, we could have oscillations for essentially all starting points, or we could have convergence to K for starting points close to K and have oscillations for starting points far from K, or we could have convergence to K for all starting points. We distinguish these three situations as *oscillation*, *local stability*, and *global stability*. We want



(a) Chaotic trajectory. (b) Web plot–quadratic map.

Fig. 1 A chaotic trajectory and its web plot; quadratic map with $r = 2.99$.

to focus on a strange but interesting observation: for all the simple population models from the literature, local stability implies global stability. The question we seek to answer is: What property do these models have in common that causes local stability to imply global stability?

We and others have investigated this question of global stability. As we will see a variety of analysis methods have been proposed, but they were all in some sense unsatisfactory. An ideal method should be strong enough to apply to all the models we will study, and be easy to apply to these models. Further, the ideal method should be psychologically satisfying in that it should explain how mathematically unsophisticated biologists could produce models in which local stability implies global stability. This could be most easily done, if one could come up with some sense of *simple* or *smooth* that applies to all the example models. In this paper, we give our solution: The example models are *well-behaved* in the sense that each can be *enveloped* by a simple kind of function, a linear fractional function.

The rest of this paper is organized as follows. Section 3 gives historical background and the necessary definitions. Section 4 proves our theorems for population models. Section 5 applies our theorems to the example models. Section 6 shows that enveloping by linear fractionals is only sufficient. Section 7 extends our results to include other functions and even discontinuous multi-functions. Section 8 discusses when local without global stability is possible. Section 9 gives a table summarizing our results for population models. Section 10 closes with some brief conclusions.

3. Background and definitions

In the most general sense, we want to study difference equations of the form

$$x_{t+1} = f(x_t)$$

but with this degree of generality, little can be said. If we require that f is a function which is defined for all values of x, then given an initial condition x_0, we can show that there is a unique solution to the difference equation, that is, x_t traces out a well-defined trajectory. To obtain stronger results, we will assume that f is continuous and has as many continuous derivatives as necessary. As we will see in the examples, we will assume even more structure for a population model. Intuitively, if there is no population now, there will be no population later. If the population is small, we expect it to be growing. If the population is large, we expect it to be decreasing. These ideas suggest that there should be an *equilibrium point* where the population size will remain constant. We expect the function f to be *single-humped*, that is, f should rise to a maximum and then decrease. For some models, f will go to 0 for some finite x, but for other models f will continually decrease toward 0.

We sum up these observations with the following definition.

A ***population model*** is a difference equation of the form

$$x_{t+1} = f(x_t)$$

where f is a continuous function from the nonnegative reals to the nonnegative reals and there is a positive number $\overline{x}$, the equilibrium point, such that

$$\begin{aligned} &f(0) = 0, \\ &f(x) > x \quad \text{for} \quad 0 < x < \overline{x}, \\ &f(x) = x \quad \text{for} \quad x = \overline{x}, \\ &f(x) < x \quad \text{for} \quad x > \overline{x}, \end{aligned}$$

and if $f'(x_m) = 0$ and $x_m \leq \overline{x}$ then

$$\begin{aligned} &f'(x) > 0 \quad \text{for} \quad 0 \leq x < x_m, \\ &f'(x) < 0 \quad \text{for} \quad x > x_m \text{ such that } f(x) > 0. \end{aligned}$$

We will allow the possibility that $f(x) = 0$ for all $x > x_\infty$ and therefore, that $f(x)$ is not strictly differentiable at x_∞. Otherwise, we assume that f is three times continuously differentiable.

We want to know what will happen to x_t for large values of t. Clearly we expect that if x_0 is near $\overline{x}$ then x_t will overshoot and undershoot $\overline{x}$. Possibly this oscillation will be sustained, or possibly x_t will settle down at $\overline{x}$. The next definitions codify these ideas. A population model is ***globally stable*** if and only if for all x_0 such that $f(x_0) > 0$ we have

$$\lim_{t\to\infty} x_t = \overline{x}$$

where $\overline{x}$ is the unique equilibrium point of $x_{t+1} = f(x_t)$. A population model is ***locally stable*** if and only if for every small enough neighborhood of $\overline{x}$, if x_0 is in this neighborhood, then x_t is in this neighborhood for all t, and

$$\lim_{t\to\infty} x_t = \overline{x}.$$

How can we decide if a model has one of these properties? The following well-known theorem gives one answer.

Theorem 1. *If* $f(x)$ *is differentiable then, a population model is locally stable if* $|f'(\overline{x})| < 1$*, and if the model is locally stable then* $|f'(\overline{x})| \leq 1$.

For global stability, a slight modification of a very general theorem of Sarkovskii (1964) gives:

Theorem 2. *A continuous population model is globally stable iff it has no cycle of period 2. (That is, there is no point except* $\overline{x}$ *such that* $f(f(x)) = x$.*)*

This theorem has been noted by Cull (1981) and Rosenkranz (1983).

Unfortunately, this global stability condition may be difficult to test. Further, there is no obvious connection between the local and global stability conditions.

Various authors have demonstrated global stability for some population models. Fisher et al. (1979) and Goh (1979) used Lyapunov functions (LaSalle, 1976) to show global stability. This technique suffers from the drawbacks that a different Lyapunov function is needed for each model and that there is no systematic method to find these functions. Singer (1978) used the negativity of the Schwarzian to show global stability. This technique does not cover all the models we will consider, and it even requires modification to cover all the models it was claimed to cover. Rosenkranz (1983) noted that no period 2 was implied by $|f'(x)f'(f(x))| < 1$ and showed that this condition held for a population genetics model. This condition seems to be difficult to test for the models we will consider. Cull (1981, 1986, 1988a,b) developed two conditions $\mathcal{A}$ and $\mathcal{B}$ and showed that each of the models we will consider satisfied at least one of these conditions. These conditions used the first through the third derivatives and so were difficult to apply. Also, as Huang (1986) pointed out these conditions required continuous differentiability. All of these methods are relatively mathematically sophisticated, and so it is not clear how biological modelers could intuitively see that these conditions were satisfied.

If we return to the condition for local stability, we see that it says if for x slightly less than 1, $f(x)$ is below a straight line with slope -1, and if for x slightly greater than 1, $f(x)$ is above the same straight line, then the model is locally stable. If we consider the model

$$x_{t+1} = x_t \mathrm{e}^{2(1-x_t)},$$

we can see that the local stability bounding line is $2 - x$. Somewhat suprisingly, this line is an upper bound on $f(x)$ for all x in $[0, 1)$ and a lower bound for all $x > 1$ (see Fig. 3). Since $2 - (2 - x) = x$, the bounding by this line can be used to argue that for this model there are no points of period 2, and by Theorem 2 the model is globally stable. From this example, we abstract the following definition.

A function $\phi(x)$ ***envelops*** a function $f(x)$ if and only if

- $\phi(x) > f(x)$ for $x \in (0, 1)$
- $\phi(x) < f(x)$ for $x > 1$ such that $\phi(x) > 0$ and $f(x) > 0$.

We will use the notation $\phi(x) \bowtie f(x)$ to symbolize this enveloping. In this definition we have simplified our notation by assuming that the fixed point is at $\overline{x} = 1$. Our example population models are all normalized to satisfy this condition. Some of our calculations will be easier with this assumption, and the form of the enveloping functions will also be simplified using this assumption.

As we will see, our example population models have one or more parameters, and a model with one choice of parameters will envelop the same model with a different choice of parameters. For example, the function $x\mathrm{e}^{2(1-x)}$ envelops all the functions of the form $x\mathrm{e}^{r(1-x)}$ for $r \in (0, 2)$.

While a straight line was sufficient to envelop $x\mathrm{e}^{2(1-x)}$, a straight line fails to envelop the closely related function $x[1 + 2(1 - x)]$. To get a more general enveloping function, we consider the ratio of two linear functions and assume that the ratio is 1 when $x = 1$ and the derivative of this function is -1 when $x = 1$, which gives the following definition.

A ***linear fractional function*** is a function of the form

$$\phi(x) = \frac{1 - \alpha x}{\alpha - (2\alpha - 1)x} \qquad \text{where } \alpha \in [0, 1)\,.$$

These functions have the properties

- $\phi(1) = 1$
- $\phi'(1) = -1$
- $\phi(\phi(x)) = x$
- $\phi'(x) < 0$.

The shape of our linear fractional functions changes markedly as α varies. For $\alpha = 0, \phi(x) = 1/x$, which has a pole at $x = 0$, and decreases with an always positive second derivative. For $\alpha \in (0, 1/2)$, $\phi(x)$ starts (for $x = 0$) at $1/\alpha$ and decreases with a positive second derivative. For $\alpha = 1/2$, $\phi(x) = 2 - x$, which starts at 2 and decreases to 0 with a zero second derivative. For $\alpha \in (1/2, 1)$, $\phi(x)$ starts at $1/\alpha$, decreases with a negative second derivative, and hits 0 at $1/\alpha$ which is greater than 1. We are only interested in these functions when $x > 0$ and $\phi(x) > 0$, so we do not care about the pole in these linear fractionals because the pole occurs outside the area of interest. Figure 2 shows the three different shapes of linear fractional functions.

4. Theorems

We are now in a position to prove the necessary theorems. In what follows, we will assume that our model is $x_{t+1} = f(x_t)$, and that the model has been normalized so that the equilibrium point is 1, that is $f(1) = 1$. We will use the notation $f^{(k)}(x)$

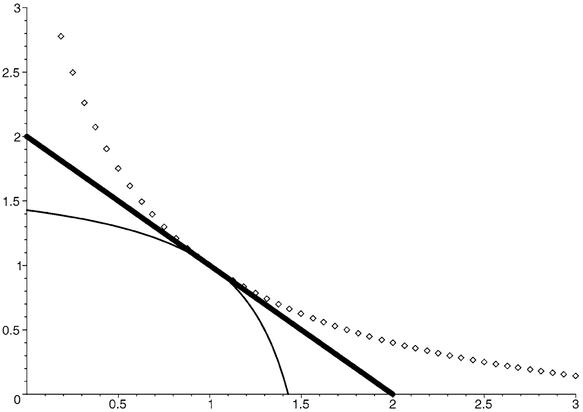


Fig. 2 Three types of linear fractionals. Dotted line $\alpha = 1/4$. Heavy line $\alpha = 1/2$. Light line $\alpha = .7$.

to mean that the function f has been applied k times to x. This notation can be recursively defined by $f^{(0)}(x) = x$ and $f^{(i)}(x) = f(f^{(i-1)}(x))$ for $i \geq 1$.

Theorem 3. *Let $\phi(x)$ be a monotone decreasing function which is positive on $(0, x_-)$ and so that $\phi(\phi(x)) = x$. Assume that $f(x)$ is a continuous function such that*

- $\phi(x) > f(x)$ on $(0, 1)$,
- $\phi(x) < f(x)$ on $(1, x_-)$,
- $f(x) > x$ on $(0, 1)$,
- $f(x) < x$ on $(1, \infty)$,
- $f(x) > 0$ on $(1, x_\infty)$,

then for all $x \in (0, x_\infty)$, $\lim_{k\to\infty} f^{(k)}(x) = 1$.

Proof: From Sarkovskii's theorem, it suffices to show that $f(x)$ has no cycle of period 2. We show that $f(f(x)) > x$ for $x \in (0, 1)$. If $f(f(x)) > 1$ then $f(f(x)) > x$. If $f(f(x)) < 1$ and $f(x) < 1$ then $f(f(x)) > f(x) > x$. If $f(f(x)) < 1$ and $f(x) > 1$, $\phi(f(x)) < f(f(x))$ and $x_- > \phi(x) > f(x)$, and since $\phi(x)$ is decreasing and self inverse $x = \phi(\phi(x)) < \phi(f(x)) < f(f(x))$. A similar argument shows that $x > f(f(x))$ for $x > 1$. (Even if $f(x) > 1$, $f(x) < x_-$ because $x_- > \phi(x)$.) Even though Sarkovskii's theorem assumes a closed interval, we are showing that there are no cycles in an open interval, and so none within the closed intervals inside the open interval. Further our assumptions on $f(x)$ allow us to argue that there is a small ε so that $f^{(k)}(x)$ will eventually fall into the closed interval $[\varepsilon, \phi(\varepsilon)]$. □

A slight recasting of the above argument gives:

Corollary 4. *If $f_1(x)$ is enveloped by $f_2(x)$, and $f_2(x)$ is globally stable, then $f_1(x)$ is globally stable.*

Corollary 5. *If $f(x)$ is enveloped by a linear fractional function then $f(x)$ is globally stable.*

A function $h(z)$ is ***doubly positive*** iff

1. $h(z)$ has a power series $\sum_{i=0}^{\infty} h_i z^i$,
2. $h_0 = 1, h_1 = 2$,
3. for all $n \geq 1$, $\quad h_n \geq h_{n+1}$,
4. for all $n \geq 2$, $\quad h_n - 2h_{n+1} + h_{n+2} \geq 0$.

Theorem 6. *Let $x_{t+1} = f(x_t)$ where $f(x) = xh(1-x)$ and $h(z)$ is doubly positive, then $f(x)$ is enveloped by the linear fractional function*

$$\phi(x) = \frac{1 - \alpha x}{\alpha + (1 - 2\alpha)x},$$

where $\alpha = \frac{3-h_2}{4-h_2} \geq \frac{1}{2}$, and the model $x_{t+1} = f(x_t)$ is globally stable.

Proof: Because the bounding for enveloping only has to hold while $\phi(x)$ is positive, we only need to consider the intervals $(0, 1)$ and $(1,\ 1/\alpha)$.

Recasting in terms of $z = 1 - x$ we want to show that $\phi(z) - (1 - z)h(z) > 0$ for $z \in (0, 1)$ and $\phi(z) - (1 - z)h(z) < 0$ for $z \in (-\frac{1}{\beta}, 0)$ where $\phi(z) = \frac{1+\beta z}{1-(1-\beta)z}$ and $\beta = \frac{\alpha}{1-\alpha} = 3 - h_2$. By assumption, $\beta \geq 3 - h_1 = 1$, and hence $1 - (1 - \beta) > 0$ for all $z \in (-1/\beta, 1)$. Therefore, it suffices to determine the sign of $1 + \beta z - (1 - z)(1 - (1 - \beta)z)h(z)$. Assuming that $h(z)$ has a power series, $g(z)$ can be written as:

$$\begin{array}{lllll}
1 & +\beta z & & & \\
-h_0 & -h_1 z & -h_2 z^2 & -h_3 z^3 & -\cdots \\
 & +(2-\beta)h_0 z & +(2-\beta)h_1 z^2 & +(2-\beta)h_2 z^3 & +\cdots \\
 & & -(1-\beta)h_0 z^2 & -(1-\beta)h_1 z^3 & -\cdots
\end{array}$$

By the assumptions on h_0 and h_1, the coefficients of z^0 and z^1 vanish. By choosing $\beta = 3 - h_2$, the coefficient of z^2 vanishes. The succeeding coefficients can be written as

$$(\beta - 1)[h_n - h_{n+1}] + [h_{n+1} - h_{n+2}],$$

with $n \geq 1$. By assumption $\beta \geq 1$. So assuming that $h_n \geq h_{n+1}$ makes all these coefficients nonnegative, and for the power series to converge at least one of these inequalities must be strict, and hence $\phi(z) - (1 - z)h(z) > 0$ for $z \in (0, 1)$. We have shown that the function $g(z)$ has the form $z^3 p(z)$, and it is *negative* on $(-1/\beta, 0)$, if $p(z)$ is positive on $(-1/\beta, 0)$. This will follow if $p_n - \frac{1}{\beta}p_{n+1} \geq 0$, where p_n and p_{n+1} are the n^{th} and $n + 1^{\text{st}}$ coefficients of $p(z)$. From above,

$$p_n - \frac{1}{\beta}p_{n+1} \;=\; (\beta - 1)[h_n - h_{n+1}] + \frac{1}{\beta}[h_{n+1} - 2h_{n+2} + h_{n+3}] \geq 0$$

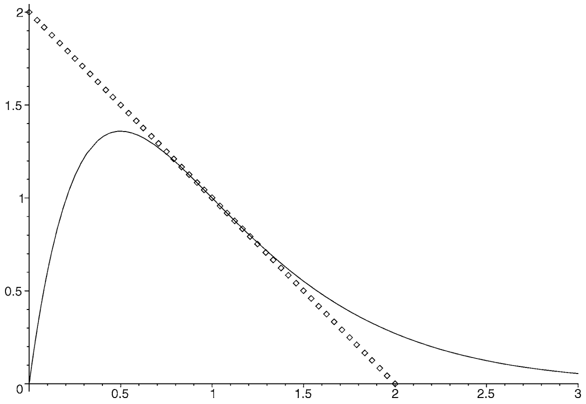


Fig. 3 Model I, $f(x_t) = x_t \mathrm{e}^{2(1-x_t)}$, is enveloped by the straight line $2 - x$ which is the linear fractional with $\alpha = 1/2$.

by the assumptions, and at least one inequality will be positive if the power series converges. □

While this doubly positive condition will be sufficient for a number of models, it is not sufficient for all the examples because, in particular, β will be less than 1 for some of the models. The following observation will be useful in many cases.

Observation 1. Let $\phi(x) = A(x)/B(x)$, $f(x) = C(x)/D(x)$ and $G(x) = A(x)D(x) - B(x)C(x)$. If $G(1) = 0$, $G'(1) = 0$, and $G''(x) > 0$ on $(0, 1)$ and $G''(x) < 0$ for $x > 1$, then $\phi(x)$ envelops $f(x)$. (We are implicitly assuming that A, B, C, D are all positive, and all functions are twice continuously differentiable.)

Proof: Obviously, if $G'(1) = 0$ and $G''(x) > 0$ on $(0, 1)$ then $G'(x) < 0$ on $(0, 1)$. Also, if $G''(x) < 0$ for $x > 1$, $G'(x) < 0$ for $x > 1$. But then $G(x)$ is always decreasing, and since $G(1) = 0$, $G(x) > 0$ for $x < 1$ and $G(x) < 0$ for $x > 1$. Rewriting this result shows that $\phi(x)$ envelops $f(x)$. □

If convenient we can switch to the variable $z = 1 - x$, and, of course, $G''(x) = G''(z)$. So if $G''(z) = zp(z)$ where $p(z)$ is strictly positive then $\phi(x)$ envelops $f(x)$.

5. Simple models of population growth

In this section we will apply the techniques of the previous section to 7 models from the literature.

5.1. *Model I*

The model $x_{t+1} = x_t \mathrm{e}^{r(1-x_t)}$ is widely used (see, for example Moran (1950); Ricker (1954); May (1974)). Our first observation is that $0 < r \leq 2$ is the necessary condition for local stability. It is easy to show that this model with $0 < r < 2$ is enveloped

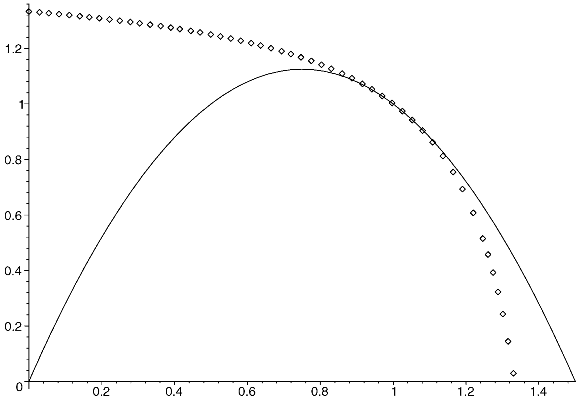


Fig. 4 Model II: The quadratic map is enveloped by $(4-3x)/(3-2x)$.

by this model with $r=2$. As we showed earlier, (see Fig. 3) this model with $r=2$ is enveloped by $\phi(x)=2-x$ and hence local and global stability coincide.

It is also easy to check that the doubly positive condition holds for this model. Specifically,

$$h(z)=\mathrm{e}^{2z}=1+2z+\frac{2^2z^2}{2!}+\frac{2^3z^3}{3!}+\cdots$$

and $h_0=1$, and $h_1=2$, and

$$h_n-h_{n+1}=\frac{2^n}{(n+1)!}[n+1-2]=\frac{2^n(n-1)}{(n+1)!}\geq 0$$

for $n\geq 1$, and

$$h_n-2h_{n+1}+h_{n+2}=\frac{2^n}{(n+2)!}[n^2-n-2]\geq 0$$

for $n\geq 2$.

5.2. *Model II*

The model $x_{t+1}=x_t[1+r(1-x_t)]$ is sometimes considered to be a truncation of Model I. (see Smith (1968)) As for Model I the necessary condition for local stability is $0<r\leq 2$. Again like Model I, it is easy to show that this model with $0<r<2$ is enveloped by this model with $r=2$. Unlike Model I, this model is not enveloped by a straight line. But the doubly positive condition holds. Specifically, $h(z)=1+2z$, so

$$h_n-h_{n+1}=\left\{\begin{matrix}2-0, & n=1\\ 0-0, & n>1\end{matrix}\right\}\geq 0,$$

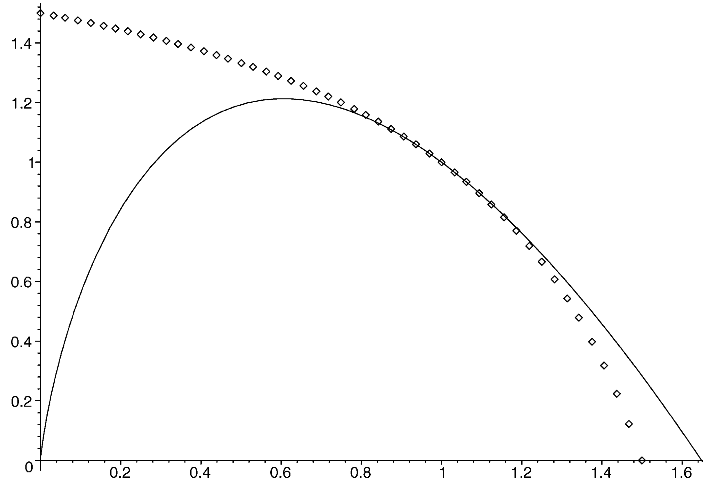


Fig. 5 Model III: $f(x) = x[1 - 2\ln x]$ enveloped by $(3 - 2x)/(2 - x)$.

and

$$h_n - 2h_{n+1} + h_{n+2} = \begin{Bmatrix} 2, & n = 1 \\ 0, & n > 1 \end{Bmatrix} \geq 0.$$

Since $h_2 = 0$, the enveloping function has $\alpha = \frac{3}{4}$ and is (see Fig. 4)

$$\phi(x) = \frac{4 - 3x}{3 - 2x}.$$

In this simple example, it's easy to check that the enveloping condition is equivalent to $(1 - x)^3$ having a single change of sign which occurs at $x = 1$.

5.3. *Model III*

The model $x_{t+1} = x_t[1 - r\ln x_t]$ is attributed to Gompertz and studied by Nobile et al. (1982). As with the preceding two models $0 < r \leq 2$ is the necessary condition for local stability, the model with $r = 2$ envelops the model with $0 < r < 2$, and the doubly positive condition holds. Specifically,

$$h(z) = 1 - 2\ln(1 - z) = 1 + 2z + \frac{2z^2}{2} + \cdots + \frac{2z^n}{n} + \cdots$$

and $h_n - h_{n+1} = \frac{2}{n(n+1)} > 0$ for $n \geq 1$ and $h_n - 2h_{n+1} + h_{n+2} = \frac{4}{n(n+1)(n+2)} > 0$ for $n \geq 1$. Since $h_2 = 1$, the enveloping function has $\alpha = 2/3$ and is $\phi(x) = \frac{3-2x}{2-x}$ (see Fig. 5).

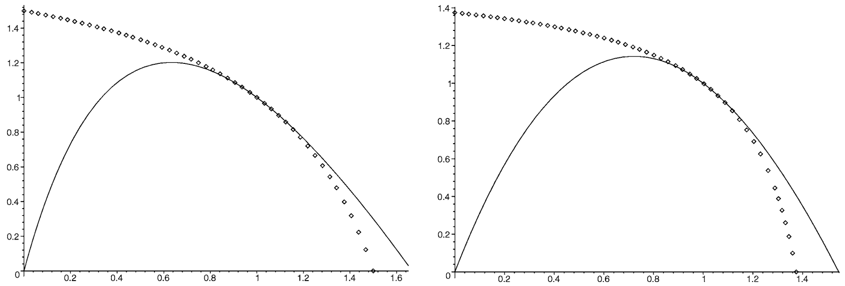


Fig. 6 Two examples of Model IV. The model with $d = 3$ is enveloped by $(3 - 2x)/(2 - x)$. With $d = 11$ the model is enveloped by $(11 - 8x)/(8 - 5x)$.

5.4. Model IV

Model IV is

$$x_{t+1} = x_t \left(\frac{1}{b + cx_t} - d \right)$$

from Utida (1957). This model differs from the previous three in that there are two parameters, b and d, remaining after the carrying capacity has been normalized to 1.

The necessary condition for local stability gives

$$\frac{d-1}{(d+1)^2} \leq b < \frac{1}{d+1}.$$

To avoid a pole for $x > 0$, we also assume, $d > 1$. It is easy to check that this model with $b = \frac{d-1}{(d+1)^2}$ envelops this model with larger values of b. With these assumptions

$$f(x) = x \left[\frac{(d+1)^2}{d - 1 + 2x} - d \right]$$

and

$$h(z) = \frac{d+1}{1 - \frac{2}{d+1} z} - d.$$

Since d > 1,

$$h(z) = 1 + 2z + \frac{2^2}{d+1} z^2 + \frac{2^3}{(d+1)^2} z^3 + \cdots$$

and

$$h_n = \frac{2^n}{(d+1)^{n-1}} \text{ for } n \geq 1.$$

So,

$$h_n - h_{n+1} = \frac{2^n}{(d+1)^n}(d-1) > 0$$

and

$$h_n - 2h_{n+1} + h_{n+2} = \frac{2^n(d-1)^2}{(d+1)^n} > 0.$$

The enveloping function is (see Fig. 6)

$$\phi(x) = \frac{4d - (3d-1)x}{3d - 1 + 2(1-d)x}$$

and has

$$\alpha = \frac{3d-1}{4d} > \frac{1}{2}.$$

We note that $\phi(x)$ has a pole, but $\phi(x)$ goes to zero before the pole, so we can simply ignore the pole. Of course, we only need $\phi(x)$ to bound $f(x)$ on the interval $(0, \frac{4d}{3d-1})$ where $\phi(x)$ is positive.

5.5. *Model V*

Model V has

$$f(x) = \frac{(1 + a\mathrm{e}^b)x}{1 + a\mathrm{e}^{bx}}$$

and comes from Pennycuick et al. (1968). This and the following two models are more complicated than the previous models because we have to consider different enveloping functions for different parameter ranges.

For $b \le 2$, $x\mathrm{e}^{b(1-x)}$ envelops $f(x)$ because $\mathrm{e}^{b(1-x)} + a\mathrm{e}^{bx} \bowtie 1 + a\mathrm{e}^b$ since $\mathrm{e}^{b(1-x)} \bowtie 1$ for $b > 0$. (Here we are using the notation $g(x) \bowtie h(x)$ to mean $g(x) > h(x)$ for $x \in (0, 1)$ and $g(x) < h(x)$ for $x > 1$ and still in the range of interest.) But $x\mathrm{e}^{b(1-x)}$ is just Model I, and as we showed it is enveloped by $2 - x$ (see Fig. 7a). So Model V is globally stable for $b \le 2$. Of course, the inequality still holds for $b > 2$, but since Model I is *not* stable for $b > 2$, the inequality does not help in establishing the stability of Model V.

For this model we assume that $a > 0$ and $b > 0$. The necessary condition for local stability gives $a(b-2)e^b \le 2$. It is easy to show that this model with larger values of a envelops this model with smaller values of a. Letting $a\mathrm{e}^b = \frac{2}{b-2}$ and using $z = 1 - x$ we have

$$f(z) = \frac{b(1-z)}{(b-2) + 2\mathrm{e}^{-bz}}.$$

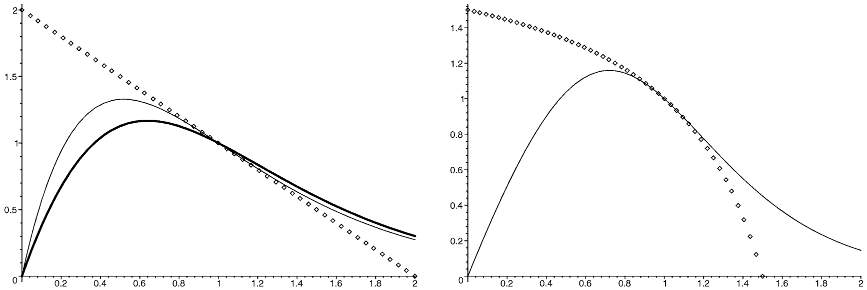


Fig. 7 Two examples of Model V. The model with $b \leq 2$ is enveloped by $(2 - x)$. (The curve becomes steeper as a is increased.) With $b = 3$ the model is enveloped by $(3 - 2x)/(2 - x)$.

The enveloping linear fractional is

$$\phi(x) = \frac{b - (b-1)x}{(b-1) - (b-2)x}$$

or converting to $z = 1 - x$,

$$\phi(z) = \frac{1 + (b-1)z}{1 + (b-2)z}.$$

Following the technique of the Observation, we have,

$$\begin{aligned} G(z) &= (b-2) + 2\mathrm{e}^{-bz} + (b-1)(b-2)z + 2(b-1)z\mathrm{e}^{-bz} \\ &\quad -b(1-z) - b(b-2)z(1-z). \end{aligned}$$

It is easy to check that $G(0) = G'(0) = 0$. Finally,

$$G''(z) = z\left\{2b(b-2)\left(\frac{1-\mathrm{e}^{-bz}}{z}\right) + 2(b-1)b^2\mathrm{e}^{-bz}\right\}.$$

Clearly, $\frac{1-\mathrm{e}^{-bz}}{z}$ is positive for all $z \neq 0$ and since $b > 2$, the first term in {-brackets is positive. Of course, the second term is also positive. So by the Observation, Model V is enveloped as claimed (see Fig. 7b).

5.6. Model VI

Model VI is from Hassel (1974) and has

$$f(x) = \frac{(1+a)^b x}{(1+ax)^b} \quad \text{with} \quad a > 0, \quad b > 0.$$

There are two cases to consider $0 < b \leq 2$ and $b > 2$. The enveloping function for $b \leq 2$ is $\phi(x) = 1/x$ (see Fig. 8a). Cross multiplication shows that we want

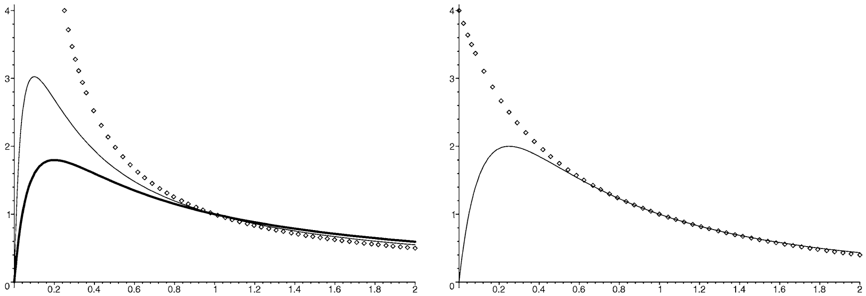


Fig. 8 Two examples of Model VI. The model with $b \leq 2$ is enveloped by $1/x$. (The curve becomes steeper as a is increased.) With $b = 3$ the model is $27x/(1+2x)^3$ and it is enveloped by $(4-x)/(1+2x)$.

$(1+ax)^b \bowtie (1+a)^b x^2$. Taking b^{th} roots and rearranging shows that we want $1 - x + ax(1 - x^{\frac{2-b}{b}}) \bowtie 0$. Clearly, each of the two terms is positive below 1 and negative above 1, and so enveloping is established.

The local stability condition implies that $a(b-2) \leq 2$. It is also is easy to show that this model with smaller values of a is enveloped by this model with larger values of a. So if $b > 2$, we can use $a = \frac{2}{b-2}$ or equivalently $b = \frac{2+2a}{a}$ to simplify formulas. The function is enveloped by a linear fractional with parameter $(b-2)/2(b-1)$. (see Fig. 8b)

Cross multiplication gives

$$\begin{aligned} G(x) = {} & 2(b-1)(1+ax)^b - (b-2)(1+ax)^b x \\ & -(b-2)(1+a)^b x - 2(1+a)^b x^2. \end{aligned}$$

Simplification, multiplication by $a/2$ and division by $(1+ax)$ gives

$$\begin{aligned} G(x) &\equiv (2+a)(1+ax)^{b-1} - x(1+ax)^{b-1} - (1+a)^b x \qquad \text{and} \\ G''(x) &\equiv (2+a)^2 a(b-2)(1+ax)^{b-3} - a(b-1)(1+ax)^{b-2} \\ & \quad -(2+a)(1+ax)^{b-2} - (2+a)a(b-2)x(1+ax)^{b-3}. \end{aligned}$$

Dividing by $(1+ax)^{b-3}$ and simplifying gives

$$G''(x) \equiv (2+a)^2 2 - 2(2+a)(1+ax) - 2(2+a)x \equiv 2(2+a)(1+a)(1-x).$$

So $G''(x) \bowtie 0$ and enveloping is established. (In this argument we use $\equiv$ to indicate that two quantaties have the same sign, but not necessarily the same value.)

A somewhat simpler argument can be given by re-arranging $G(x)$ into the equivalent form

$$G(x) \equiv (1+a)[(1+ax)^{b-1} - (1+a)^{b-1}x] + (1-x)(1+ax)^{b-2}$$

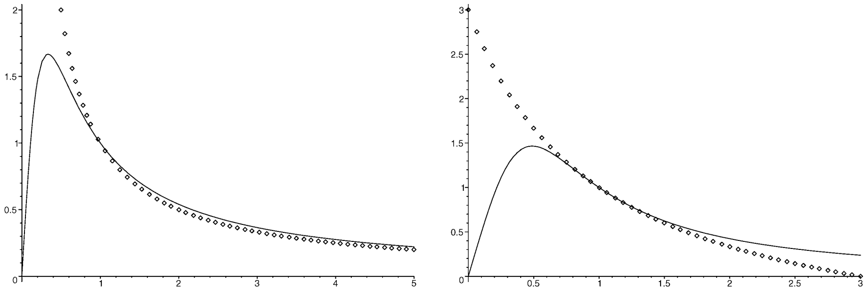


Fig. 9 Different linear fractionals envelop Model VII with different parameter values. The fractional $1/x$ is used for $c = 2$. The fractional $(3 - x)/(1 + x)$ is used with $c = 2.5, r = 5$.

and noticing that the term in [-brackets and $1 - x$ are both positive for $x < 1$ and both negative for $x > 1$, assuming that $b > 2$.

5.7. *Model VII*

Model VII is due to Maynard Smith (1974) and has

$$f(x) = \frac{rx}{1 + (r - 1)x^c}.$$

This seems to be the hardest to analyze model in our set of examples. For example, this model does not satisfy the Schwarzian derivative condition or Cull's condition $\mathcal{A}$. Even for our enveloping analysis, we will need to consider this model as three subcases.

Similar to previous models, local stability implies $r(c - 2) \leq c$, and it is easy to show that this model with smaller values of r is enveloped by this model with larger values of r.

We first consider the situation when $c \in (0, 2]$. Here, local stability does not place an upper bound on r. Of course, we assume $r > 1$ for this to be a population model. The enveloping function here is $\phi(x) = 1/x$, that is the linear fractional with $\alpha = 0$ (see Fig. 9a). Cross multiplication shows that we need

$$1 + (r - 1)x^c - rx^2 \bowtie 0$$

for enveloping. Rewriting this gives $1 - x^c + rx^c(1 - x^{2-c}) \bowtie 0$. Clearly, $1 - x^c > 0$ and $1 - x^{2-c} \geq 0$ for $1 > x$ and $2 \geq c$, and $1 - x^c < 0$ and $1 - x^{2-c} \leq 0$ for $1 < x$ and $2 \geq c$, so enveloping is established.

For $c > 2$, we use $r = \frac{c}{c-2}$, and show that

$$\phi(x) = \frac{c - 1 - (c - 2)x}{c - 2 - (c - 3)x}$$

is the enveloping function (see Fig. 9b). As before, we calculate

$$\begin{aligned}
G(x) &= 2x^c[(c-1)-(c-2)x]+(c-1)(c-2)\\
&\quad -2(c-1)(c-2)x+c(c-3)x^2\\
G'(x) &= 2x^{c-1}[c(c-1)-(c+1)(c-2)x]-2(c-1)(c-2)+2c(c-3)x\\
G''(x) &= 2x^{c-2}[c(c-1)^2-c(c+1)(c-2)x]+2c(c-3)\\
&= 2c\{(c-1)^2x^{c-2}[1-x]+(c-3)[1-x^{c-1}]\}.
\end{aligned}$$

So for $c \geq 3$, $G''(x) \bowtie 0$ and $\phi(x)$ envelops $f(x)$.

We are left with the case when $c \in (2,3)$.

$$\frac{G''(x)}{2c} = -(c+1)(c-2)x^{c-1}+(c-1)^2x^{c-2}-(c-3)$$

and so, $G''(x)$ has two positive real roots. One of these is, of course, the root at $x=1$. Now, taking another derivative, $G''(x)$ is clearly decreasing at $x=1$, and hence the other root occurs for some $x<1$. Since $G''(0)<0$, G'' will start out negative, become positive, and then become negative for all $x>1$. But now consider $G'(x)$. $G'(0)<0$ and so while G'' is negative, G' will become more negative, and when G'' becomes positive, G' will increase from a negative value up to 0 at $x=1$, and then since $G''<0$, G' will decrease and stay negative. Hence G which starts positive will decrease through 0 at $x=1$ and continue decreasing. So, $G(x) \bowtie 0$ and $\phi(x)$ does envelop $f(x)$.

6. Enveloping by a linear fractional is only sufficient

Here we want to give a simple model which has global stability, but cannot be enveloped by any linear fractional. Define $f(x)$ by

$$f(x) = \begin{cases} 6x & 0 \leq x < 1/2 \\ 7-8x & 1/2 \leq x < 3/4 \\ 1 & 3/4 \leq x. \end{cases}$$

(see Fig. 10a) then $x_{t+1}=f(x_t)$ has $x=1$ as its globally stable equilibrium point because if $x_t \geq 1$ then $x_{t+1}=1$, for $x_t \in [1/2,1)$, $x_{t+1}>1$ and $x_{t+2}=1$, and for $x_t \in (0,1/2)$, the subsequent iterates grow by multiples of 6 and eventually surpass $1/2$. This $f(x)$ cannot be enveloped by a linear fractional because $f(1/2)=3$ which implies that the linear fractional would have $\alpha \leq -1$ and hence have a pole in $(0,1)$ and thus it could not envelop a positive function. On the other hand, the self-inverse function

$$\phi(x) = \begin{cases} 5-4x & x \leq 1 \\ (5-x)/4 & x > 1 \end{cases}$$

does envelop $f(x)$ and so demonstrates global stability.

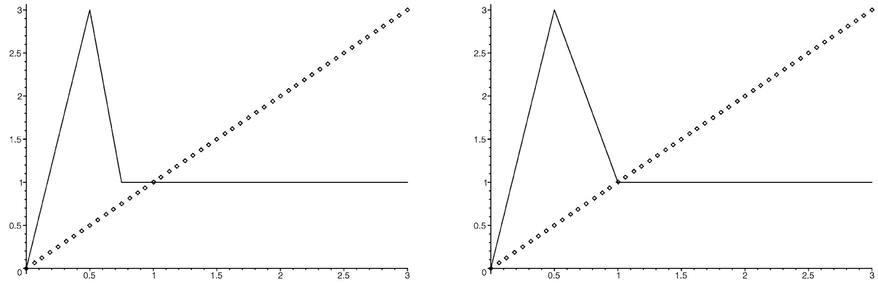


Fig. 10 Two globally stable maps which *cannot* be enveloped by linear fractionals. The second map is *not* locally stable.

The similar example (see Fig. 10b),

$$f_2(x) = \begin{cases} 6x & 0 \le x < 1/2 \\ 5 - 4x & 1/2 \le x < 1 \\ 1 & 1 \le x \end{cases}$$

also shows that enveloping by a linear fractional is not necessary for global stability. But, it also shows the somewhat suprising result that global stability does *not* imply local stability. The reason for this anomaly is our somewhat informal definition of local stability. The use of a more precise but more complicated definition (see LaSalle (1976)) would show that that this model is locally stable. Briefly, the difficulty is that if the iteration is started near but slightly below the fixed point, the next iteration is above the fixed point and further away than the starting point.

This sort of behavior is not limited to this concocted example. In all of the models, when $|f'(1)| < 1$ there is evident local convergence to the fixed point and the deviation after n steps is $O(|f'(1)|^n)$, that is, the iterates are converging to the fixed point exponentially rapidly. But, when $f'(1) = -1$ the behavior will be rather different. A much slower convergence can be expected. For example, if we take $r = 2$ in Model II, The deviation after n steps is only $O(\frac{1}{\sqrt{n}})$. So, after a million iterations, the deviation from the fixed point may only be one thousandth and another million iterations will only divide this deviation by about 1.4. A graph of these iterates will look much more like a stable period 2 cycle than a converging sequence.

7. Extensions

The previous sections have worked with the usual applied math assumption that real phenomena are as smooth and as differentiable as necessary to get a good theorem or estimate. Of course, everyone who has ever applied mathematics knows that this assumption is false, but they also know that it serves as a useful "rule of thumb." That is, in some cases the smoothness assumption may lead to bad

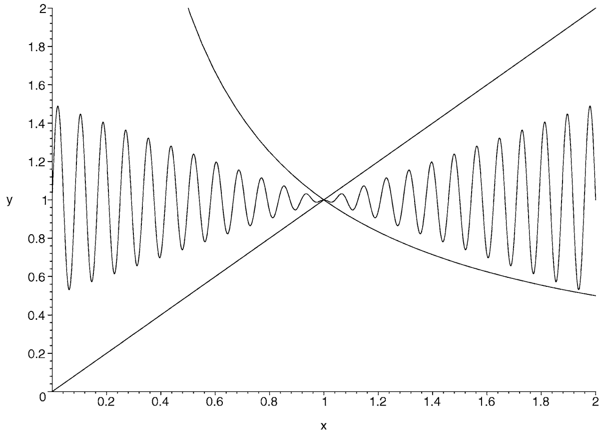


Fig. 11 An example of a highly oscillatory function. The function is bounded between $1/x$ and x and is thus globally stable even though it does not have the single-humped form.

estimates, but in many, many cases the smooth estimate is very close to observed (experimental) values. In a few cases, a result which was initially proved assuming smoothness has been shown to hold when some of the smoothness assumptions are dropped. Here we want to show that **enveloping implies global stability** does *not* require continuity, even though we originally assumed continuity. Further, the assumption that x_{t+1} is a *function* of x_t is also superfluous. The enveloping result will also hold for *multi-functions*. These extensions have slightly more complicated proofs and they require the extra assumption of *no limit points*.

The function in Fig. 11 may be atypical for population models, but such behavior may be possible in some biochemical models. The point is, of course, that enveloping is a very general technique. Here, we've still used enveloping by a linear fractional but as the general theorem states other functions can be used for enveloping. We've stuck with linear fractionals because they are sufficient for the usual population models, and because linear fractionals are easy to work with.

7.1. Multi-functions

In a population how does the size of the present population depend on the recent population size? In our simple models, we assume functional dependence, that is, in the model $x_{n+1} = f(x_n)$, we assume that $f(x_n)$ is a **function** which means that for each value of x there is exactly one value of $f(x)$. We all know that this is an over simplification. For example, if in year y the population had size p, and in year $y+7$ the population again has size p, the simple model predicts that the population sizes in years $y+1$ and $y+8$ will be the same, but no biologist would be surprised if this is false. More reasonably, a biologist would give a range of values and expect the population sizes in years $y+1$ and $y+8$ to each fall somewhere within this range.

We can model this range behavior by generalizing $f(x)$ from a function to a **multi-function**, that is, for each x, we'll assume that the multi-function $f(x)$ gives a non-empty set of values. Now our model $x_{n+1} = f(x_n)$ means that if x_n is the

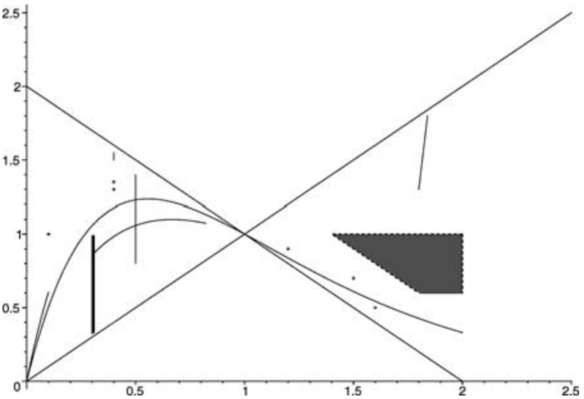


Fig. 12 An example of a multi-function. There are curves, dots, lines, and solid blocks which are all part of the multi-function. Because the multi-function is bounded between $2 - x$ and x and has no other limit points, $x = 1$ is the globally stable fixed point.

present size, then the new size x_{n+1} is somewhere in the set $f(x_n)$. There is no reason to assume that $f(x)$ is an interval of values, but for our applications we want to assume that $f(x)$ has upper and lower bounds. Here $f(x) > y$ means that every element in the set $f(x)$ is greater than the value y. Of course, we have the corresponding meaning for upper bounds. Figure 12 shows a multi-function for which $x = 1$ is the globally stable fixed point.

7.2. General theorem

For discontinuous functions (or multifunctions) we have to sharpen the idea of *enveloping* to make sure of *strict* inclusion of the function in the "wedges" between $y = \phi(x)$ and $y = x$. For an interval (a, b) on which $f(x)$ has a single fixed point p, we want the bounding

- $\phi(x) > f(x) > x$ for $x \in (a, p)$,
- $\phi(x) < f(x) < x$ for $x \in (p, b)$,

and to avoid limiting points of $f(x)$ on either $\phi(x)$ or on x, except at the fixed point p, we assume that for every sequence $\langle x \rangle$,

- if $\lim_{\langle x \rangle \longrightarrow q} f(x) = q$ then $q = p$, and
- if $\lim_{\langle x \rangle \longrightarrow q} f(x) = \phi(q)$ then $q = p$.

We say the $f(x)$ is *enveloped* by $\phi(x)$ on the interval (a, b) containing p when this strict bounding holds on the whole interval.

Theorem 7. *Assume that $f(x)$ maps the interval (a, b) into itself. ($f(x)$may be discontinuous or may be a multifunction.) Further assume that $f(p) = p$ is the unique fixed point of f in this interval, and that there is a continuous self-inverse function $\phi(x)$ which* **envelops** *$f(x)$ on (a, b). Then if x_0 is any initial point in this* *interval and* $\langle x_n \rangle$ *is any sequence consistent with* $x_{t+1} = f(x_t)$ *then* $\langle x_n \rangle$ *converges to* p*.*

Proof: Let x_0 be any initial point, then the sequence $x_0, x_1, x_2, \ldots$ naturally breaks into two subsequences, those iterates less than p and those iterates greater than p. (Of course, if some iterate x_k is p, then the sequence has $x_n = p$ for all $n \geq k$). Clearly if the sequence consists of only one of these subsequences, say $x_n < p$, then from $f(x) > x$, the sequence is bounded and increasing and has a limit, but this limit must be p, since by assumption there are no other limit points. (A similar argument holds for $x_n > p$). If the sequence $\langle x \rangle$ has a subsequence less than p and a subsequence greater than p, let us call these subsequences respectively $\langle a \rangle$ and $\langle b \rangle$. We show that $\langle a \rangle$ and $\langle b \rangle$ are monotone sequences. Assume that $(x_0, \ldots, x_k)$ are less than p, that $(x_{k+1}, \ldots, x_{k2})$ are greater than p, and that $x_{k2+1} < p$. By enveloping

$$\begin{aligned} x_{k+1} &= f(x_k) < \phi(x_k) \\ x_{k2+1} &= f(x_{k2}) > \phi(x_{k2}), \end{aligned}$$

but $\phi(x_k) > x_{k+1} > \cdots > x_{k2}$ because $x > f(x)$ for $x > p$. Since $\phi(x)$ is self-inverse and decreasing

$$x_k = \phi(\phi(x_k)) < \phi(x_{k2}) < f(x_{k2}) = x_{k2+1}.$$

So $\langle a \rangle$ is an increasing bounded sequence. By a similar argument $\langle b \rangle$ is a decreasing bounded sequence. So $\langle a \rangle$ has a limit, say L, and $\langle b \rangle$ has a limit, say U.

Next we break $\langle a \rangle$ into two subsequences $\langle a1 \rangle$ and $\langle a2 \rangle$ where if $a \in \langle a1 \rangle$ then $f(a) < p$
and if $a \in \langle a2 \rangle$ then $f(a) > p$.
Then $\lim_{\langle a1 \rangle \longrightarrow L} f(a) = L$ and by enveloping $L = p$.
On the other hand, $\lim_{\langle a2 \rangle \longrightarrow L} f(a) = U$ because for each $a \in \langle a2 \rangle$, $f(a) \in \langle b \rangle$.
By enveloping, $\phi(a) > f(a)$, so

$$\lim_{\langle a2 \rangle \longrightarrow L} \phi(b) \geq \lim_{\langle a2 \rangle \longrightarrow L} f(a) = U$$

and since ϕ is continuous $\phi(L) \geq U$.

Similarly to our handling of $\langle a \rangle$, we break $\langle b \rangle$ into two subsequences $\langle b1 \rangle$ and $\langle b2 \rangle$, and have $\lim_{\langle b1 \rangle \longrightarrow U} f(b) = U$ which by enveloping implies $U = p$. For $\langle b2 \rangle$ we have $\lim_{\langle b2 \rangle \longrightarrow U} f(b) = L$, since each $f(b)$ is in $\langle a \rangle$. By enveloping, for each $b \in \langle b2 \rangle$, $f(b) > \phi(b)$ so

$$L = \lim_{\langle b2 \rangle \longrightarrow U} f(b) \geq \lim_{\langle b2 \rangle \longrightarrow U} \phi(b) = \phi(U).$$

Thus we have both $\phi(L) \geq U$ and $L \geq \phi(U)$. Using the fact that $\phi(x)$ is decreasing and self-inverse gives $L = \phi(U)$ and $U = \phi(L)$.

But then

$$\lim_{\langle a2\rangle \longrightarrow L} f(a) = U = \phi(L) \qquad \text{implies} \qquad L = p$$

and similarly

$$\lim_{\langle b2\rangle \longrightarrow U} f(b) = L = \phi(U) \qquad \text{implies} \qquad U = p.$$

Hence, regardless of the starting x_0 the sequence $\langle x_n \rangle$ will converge to p. □

The following example shows what can happen when the hypotheses of this theorem are not satisfied. Consider the recurrence $x_{t+1} = f(x)$ with

$$f(x) = \begin{cases} 0 & x \le 0 \\ 2 - x - (x - \frac{3}{4})^2 & 0 < x < \frac{3}{4} \\ (3 - x)/2 & \frac{3}{4} \le x \le \frac{5}{4} \\ 2 - x + (x - \frac{5}{4})^2 & \frac{5}{4} < x < 2 \\ 0 & 2 \le x. \end{cases}$$

If x_0 is in the interval [3/4, 5/4] the sequence of iterates will converge to 1. I.e., $x = 1$ is a locally stable fixed point, and it is the only fixed point. But, if x_0 is chosen slightly below 3/4 or slightly above 5/4, then the sequence will oscillate above 5/4, below 3/4 endlessly, and approach the non-existent cycle

$$3/4 \longleftrightarrow 5/4.$$

This funny behavior can only occur because $f(x)$ is discontinuous. This $f(x)$ cannot be enveloped by *any* continuous self-inverse decreasing $\phi(x)$ because, as it's easy to show, such a $\phi(x)$ would have $\phi(3/4) = 5/4$ and $f(x)$ would have to have a limiting point on $\phi(x)$ at $x = 3/4$. The theorem's assumption that the only limit point of $f(x)$ on $\phi(x)$ is at the fixed point rules out this limiting periodic behavior.

7.3. Some Newton iterations

For some non-population examples, we'll consider the Newton iterations for square root and for reciprocal. As is well known (Cull et al. (2005)), $\sqrt{A}$ can be computed by the iteration

$$x_{t+1} = \frac{x_t^2 + A}{2x_t}.$$

Clearly this iteration has $\sqrt{A}$ as its sole fixed point on $(0, \infty)$ and the continuous function obeys

$$f(x) > x \quad \text{on} \quad (0, \sqrt{A})$$
$$f(x) < x \quad \text{on} \quad (\sqrt{A}, \infty).$$

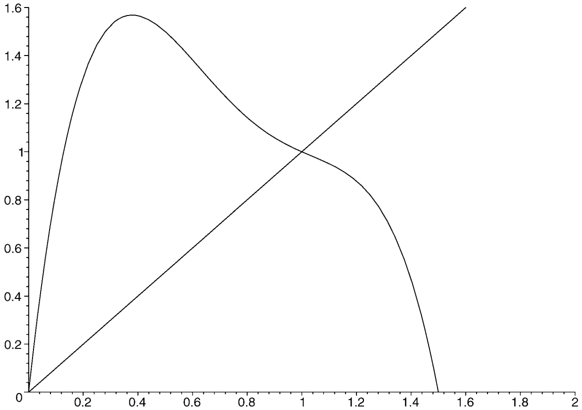


Fig. 13 Population model which is locally but not globally stable. $f(x) = x(x - 3/2)(-2 - (x - 1) - 6(x - 1)^2)$. The function $f(x)$ must have degree ≥ 4 for local *without* global stability.

We take $\phi(x) = A/x$ and it's easy to check that $\phi(x)$ does envelop $f(x)$ on $(0, \infty)$. So we conclude that for any $x_0 \in (0, \infty)$, this Newton iteration will converge to $\sqrt{A}$.

For a slightly more complicated example, we use the well known (Cull et al. (2005)) iteration

$$x_{t+1} = x_t(2 - Ax_t).$$

to compute $1/A$. Here $f(x)$ has $1/A$ as its sole fixed point in $(0, 2/A)$. Notice that $f(0) = f(2/A) = 0$ so this iteration will not converge to $1/A$ when it is started at either of these points. We can take the straight line $\phi(x) = 2/A - x$ and show that this $\phi(x)$ does envelop $f(x)$ on $(0, 2/A)$ and hence that this iteration converges to $1/A$ when started at any point within $(0, 2/A)$.

8. Locally stable but not globally stable examples

The following two examples show that the simple assumption that a population model is described by a one-humped curve, is not sufficient for local stability to imply global stability. On the other hand these examples do not show the *smoothness* of the usual models. The reason for this discrepancy is that these examples are more complicated algebraically than the usual models. The simplicity of the usual models permits their enveloping by linear fractional functions. A reasonable contention is that a "free-hand" drawing of a one-humped curve would not produce the "bends" or "kinks" shown in these examples. This contention led to the series of papers which attempted to find a simple geometric reason for local stability to imply global stability. While we believe that enveloping by a linear fractional is a simple geometric condition, we also want to argue that algebraic simplicity also plays a role in the usual models.

In a sense Model II is the simplest population model. It is a 2nd degree polynomial, and clearly no smaller degree polynomial could show the humped form. What happens when we consider a 3rd degree polynomial? Following the proof of Theorem 6 we can show that a linear fractional with $\alpha = (3 - h_2)/(4 - h_2)$ will envelop such a population model. We do need that $3 > h_2$, but we actually have $1 \geq h_2$ because otherwise $f(x)$ would eventually increase and have a second fixed point. Fourth degree polynomial is possible. Our point is that the usual models are algebraically *buffered* in the sense that slightly increasing the algebraic complexity will not change the local implies global implication. Singer (1978) also used his negative Schwarzian condition to show that local stability implies global stability for degree 3 polynomial models.

This "buffering" also holds for other models. For example, in Model I, there is a first degree polynomial in the exponent. We can create a more complicated population model by increasing the degree of this polynomial. Specifically for a second degree polynomial we have

$$f(x) = x\mathrm{e}^{2(1-x)+\gamma(1-x)^2}$$

where γ is not yet specified. If γ were positive, there would be a second fixed point because the exponent would be eventually increasing in x. So we may assume the $\gamma \leq 0$. We claim that $1/x$ envelops $f(x)$. We show this by showing that 1 envelops $xf(x)$. Clearly $1 > xf(x)$ for $x = 0$ and $1 = xf(x)$ for $x = 1$. The derivative of $xf(x)$ after some re-arrangement is

$$2x(1 - x)[1 - \gamma x].$$

Since $\gamma \leq 0$, $xf(x)$ is increasing on $(0, 1)$ and decreasing for $x > 1$. With the previous statement this shows that $1 \bowtie xf(x)$, and hence that $1/x \bowtie f(x)$. We conclude that if we try to generalize Model I to a model of the form

$$f(x) = x\mathrm{e}^{q(x)},$$

then local stability implies global stability if the degree of $q(x)$ is less than or equal to 2. As Fig. 14 shows, when $q(x)$ has degree 3, it is possible to construct a population model which is locally stable, but not globally stable.

It's easy to see that that these two example do not show global stability. For the example in Fig. 13, a population crash is possible. Pick x_t to get the maximum response, e.g. $x_t \approx .4$, gives $x_{t+1} \approx 1.6$, but then $x_{t+2} = 0$ and the population has died out. Of course, picking $x_t \approx 1$ will give spiral convergence to $x = 1$.

The example in Fig. 14 does not show a population crash. Instead it has a period 2 cycle. If $x_t = x_M$, where $f(x_M)$ is the maximum, then $x_t > 1$ but $x_{t+2} = x_M = x_t$. This period 2 cycle is locally stable, starting with x_t near x_M the sequence of iterates will converge to the cycle. On the other hand, starting with x_t near 1 will give convergence to $x = 1$. These two convergence regions are separated by an unstable period 2 cycle. That is, there are two points $z_1 < 1$ and $z_2 > 1$ so that $f(z_1) = z_2$

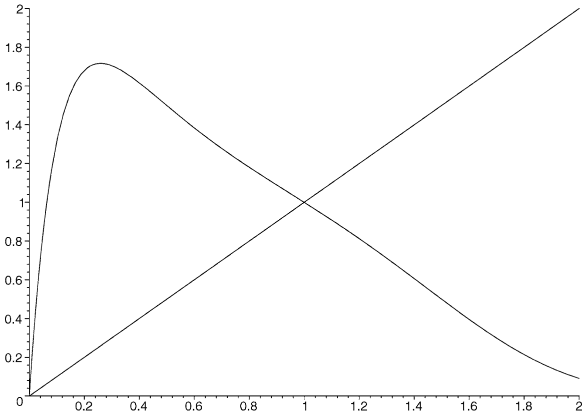


Fig. 14 A population model which is locally but not globally stable. $f(x) = x\mathrm{e}^{-q(x)}$ with $q(x) = 1.9(x-1) - (7.6 - 8\ln 3)(x-1)^3$. The function $q(x)$ must have degree ≥ 3 for local *without* global stability.

and $f(z_2) = z_1$, and if x_0 is picked in $(z_1, 1)$ then x_t will converge to 1, while if x_0 is chosen in (x_M, z_1) the iterates will converge to the period 2 cycle containing x_M.

There is also an unstable period 2 cycle, $z_1 \leftrightarrow z_2$, in Fig. 13. For x_0 in $(z_1, 1)$ the iterates will converge to 1, while for x_0 in (x_M, z_1) the iterates will go to a population crash.

This discussion should show by example that that the usual population models are "buffered" algebraically, so that making the functions slightly more complicated still does not permit local stability without global stability. Biologists haven't just been "lucky" when they showed local stability and then assumed global stability. They have chosen functions which are geometrically smooth enough to allow enveloping by linear fractional functions and are algebraically simple enough to be "buffered" against counter-intuitive behavior.

9. Summary table

The following table summarizes the stability conditions for the seven population models. It contains the models, their parametric regions of stability, references to the original sources, and the bounding linear fractionals. The column marked Theorems indicate which earlier methods could be used to show global stability for the model. The letters $\mathcal{A}$ and $\mathcal{B}$ refer to the two methods in Cull (1988b), the letter $\mathcal{S}$ refers to the negative Schwarzian condition of Singer (1978).

The following observations are from Heinschel (1994). Cull's paper (Cull, 1988a) indicated that Model V satisfies the conditions of Theorems $\mathcal{A}$ and $\mathcal{B}$. However, upon studying the details of the model, we find that Model V satisfies the conditions of Theorem $\mathcal{B}$, but not those of Theorem $\mathcal{A}$. Also, Singer's paper (Singer, 1978) states that Model VI satisfies the condition that the Schwarzian derivative is negative for all x when $b > 1$, which is not true. However, for global stability the

Table 1

Model number	Function	Parametric region for stability	Theorems	References	Bounding Linear Fractionals
I	$f_1(x) = x\mathrm{e}^{r(1-x)})$	$0 < r \le 2$	$\mathcal{A}, \mathcal{B}, \mathcal{S}$	Fisher et al. (1979), May (1974), Moran (1950), Ricker (1954)	$2 - x$
II	$f_2(x) = x(1 + r(1 - x))$	$0 < r \le 2$	$\mathcal{A}, \mathcal{B}, \mathcal{S}$	May (1976), Smith (1968)	$(4 - 3x)/(3 - 2x)$
III	$f_3(x) = x(1 - r \ln x)$	$0 < r \le 2$	$\mathcal{A}$	Nobile et al. (1982)	$(3 - 2x)/(2 - x)$
IV	$f_4(x) = x(\frac{1}{b+cx} - d)$	$\frac{d-1}{(d+1)^2} \le b < \frac{1}{d+1}$	$\mathcal{A}, \mathcal{S}$	Utida (1957)	$(11 - 8x)/(8 - 5x)$
V	$f_5(x) = \frac{(1+a\mathrm{e}^b)x}{1+a\mathrm{e}^{bx}}$	$0 < a, 0 < b,$ $a(b-2)\mathrm{e}^b \le 2$	$\mathcal{B}, \mathcal{S}$	Pennycuick et al. (1968)	$2 - x$ for $b \le 2$ $\frac{b-(b-1)x}{(b-1)-(b-2)x}$ for $b \ge 2$
VI	$f_6(x) = \frac{(1+a)^b x}{(1+ax)^b}$	$0 < a, 0 < b,$ $a(b-2) \le 2$	$\mathcal{B}$, Modified $\mathcal{S}$	Hassel (1974)	$1/x$ for $b \le 2$ $\frac{2(b-1)-(b-2)x}{(b-2)+2x}$ for $b \ge 2$
VII	$f_7(x) = \frac{rx}{1+(r-1)x^c}$	$r(c-2) \le c$	$\mathcal{B}$	Smith (1974)	$1/x$ for $c \le 2$ $\frac{c-1-(c-2)x}{c-2-(c-3)x}$ for $c \ge 2$

Schwarzian only has to be negative for part of the range of x. We call this condition modified $\mathcal{S}$, and Model VI does satisfy modified $\mathcal{S}$.

10. Conclusion

Analysts would like to look at a system and predict its future. There are reasonable analysis techniques for linear systems, but there are few reasonable techniques for nonlinear systems. In this paper, we have shown that by limiting the dimension to one and considering models that have actually been used in biology, we can find some reasonable analytic techniques.

Specifically, we showed that one-dimensional difference equations whose right hand side can be enveloped by a linear fractional function are globally stable. Further, for the example biological models, enveloping is possible exactly when the model is locally stable. The enveloping technique is not limited to our example population models. As Theorem 6 shows, the infinite family of functions which satisfy the *doubly positive* conditions can all be enveloped by specific easy-to-find linear fractionals.

This idea of enveloping captures the idea of a curve being *well-behaved*. Try drawing a curve which starts at the origin, rises to a maximum, goes through $(1, 1)$ with a slope at least -1, and then goes to or toward 0. If this curve does not correspond to a globally stable model, your eye can see some odd behavior. Cull (1981, 1988b) has drawings of such curves. Figures 13 and 14 show such functions with their visible "bends" and "kinks." On the other hand, if your curve looks well-behaved, you should be able to draw a linear fractional curve that envelops it.

One surprise in our analysis is that the *one-humped* form is **not** essential. A function can have many humps and still be enveloped. So the technique we have developed is actually applicable to a wider variety of models. As we showed in Section 7, **enveloping implies global stability** holds even for discontinuous multi-functions. Thus a biologist with only a sampling of data can try enveloping without fitting a continuous curve to the data.

Another indication that biologists have very well-behaved functions in mind is that the examples are *buffered* in that making the functions slightly more complicated still leaves local stability implying global stability. In Section 8, we showed that for Models I and II increasing the degree of the polynomial by 1 still gives local stability implies global stability, but increasing the degree of the polynomial by 2 allows local stability without global stability.

More details about linear fractional functions as dynamic system is in Cull (2002). Enveloping is also discussed in Cull and Chaffee (2000a,b), and in Cull (2003).

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