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STABILITY IN ONE-DIMENSIONAL MODELS

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ABSTRACT. One dimensional nonlinear difference equations have been used to model a variety of biological phenomena including population growth. The standard biological models have the interesting characteristic 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.

1 Background and Definitions For our purposes a ***one-dimensional 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:

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

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 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 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.

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Theorem 1. *If $f(x)$ is differentiable then, a 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 [17] gives:

Theorem 2. *A continuous 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[1] and Rosenkranz[16].

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* [6] and Goh [7] used Lyapunov functions[10] 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 [18] 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 [16] 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 [1, 2, 4, 3] developed two conditions **A** and **B** and showed that each of the models we will consider satisfied at least one of these conditions. These conditions used the first through third derivatives and so were difficult to apply. Also, as Hwang [9] 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

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

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 $x > 1$. 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 hence 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.

For more complicated f's we will use linear fractionals as the enveloping functions. 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. An analysis of difference equations in which $f(x)$ is a general linear fractional appears in Cull [5].

2 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 $f(1) = 1$.

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 $x \in (0, x_\infty)$, $\lim_{k\to\infty} x_k = 1$.

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 x_k will eventually fall into the closed interval $[\varepsilon, \phi(\varepsilon)]$. ☐

A slight recasting of the above argument gives:

Corollary 1. *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 2. *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 4. *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. 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 $z \in (-\frac{1-\alpha}{\alpha}, 0)$ where $\phi(z) = \frac{1+\beta z}{1-(1-\beta)z}$ and $\beta = \frac{\alpha}{1-\alpha}$. Assuming that $h(z)$ has a power series, the function we want to bound 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 assumption 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 $\beta = 3 - h_1 \geq 3 - h_1 = 1$. 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 has the form $z^3 p(z)$, so to show that it is *negative* on $(-1/\beta, 0)$, which will follow if $p(z)$ is positive on $(-1/\beta, 0)$ and 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 $n+1^{st}$ coefficients of $p(z)$. From above, this is

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

which will be nonnegative 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.

Theorem 5. *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 $f(x)$. □

3 Some Examples

In this section we will apply the techniques of the previous section to 7 models from the literature, and also show that enveloping is not necessary for global stability.

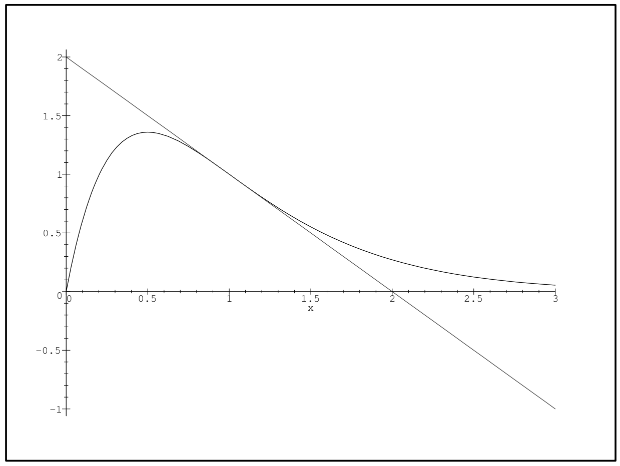

Figure 1: Model 1 with r=2, enveloped by the linear fractional $2 - x$.

3.1 Model I The model $x_{t+1} = x_t e^{r(1-x_t)}$ is widely used (see, for example [11, 12, 15]). 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 by this model with $r = 2$. This model with $r = 2$ is enveloped by 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.

3.2 Model II The model $x_{t+1} = x_t[1 + r(1 - x_t)]$ is widely used [19] and is sometimes considered to be a truncation of Model I. As for Model I the necessary condition for local stability is $0 < r \leq 2$, and 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. The enveloping function has $\alpha = \frac{3}{4}$ and is

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

3.3 Model III The model $x_{t+1} = x_t[1 - r \ln x_t]$ is attributed to Gompertz and studied by Nobile *et al* [13]. 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. The enveloping function is $\phi(x) = \frac{3-2x}{2-x}$ and has $\alpha = 2/3$.

3.4 Model IV Model IV is

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

from [21]. 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

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

which is doubly positive. The enveloping function is

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

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. since we only need $\phi(x)$ to bound $f(x)$ on the interval $(0, \frac{4d}{3d-1})$ where $\phi(x)$ is positive.

3.5 Model V

Model V has

$$f(x) = \frac{(1 + ae^b)x}{1 + ae^{bx}}$$

and comes from Pennycuick *et al* [14]. This and the following two model are more complicated than the previous models because we have to consider different enveloping functions for different parameter ranges.

For $b \leq 2$, $xe^{b(1-x)}$ envelops $f(x)$ because $e^{b(1-x)} + ae^{bx} \bowtie 1 + ae^b$ since $e^{b(1-x)} \bowtie 1$ 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 $xe^{b(1-x)}$ is just Model I, and as we showed it is enveloped by $2 - x$. So Model V is globally stable for $b \leq 2$. 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 $a(b-2)e^b \leq 2$. It is easy to show that this model with larger values of a envelops this model with smaller values of a. Letting $ae^b = \frac{2}{b-2}$ and using $z = 1 - x$ we have

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

The enveloping linear fractional is

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

which can be verified using Theorem 5.

3.6 Model VI

Model VI is from Hassel [8] and has

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

There are two cases to consider $0 < b \leq 2$ and $b > 2$. The enveloping function for $b \leq 2$ is $\phi(x) = 1/x$.

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 $b = \frac{2+2a}{2}$ to simplify formulas. Then one can show using the method of Theorem 5 that this model is enveloped by the linear fractional with $\alpha = \frac{b-2}{2(b-1)}$.

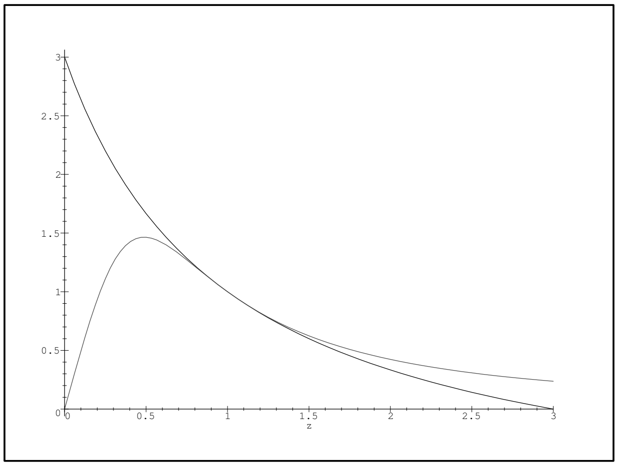

Figure 2: Model VII with c=2.5 showing envelopment by a linear fractional.

3.7 Model VII Model VII is due to Maynard Smith [20] 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 **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, but we will assume that $r > 1$. It is easy to show that $1/x$, the linear fractional with $\alpha = 0$ is the enveloping function here.

For $c > 2$, we use $r = \frac{c}{c-2}$, and use the method of Theorem 5 to show that

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

is the enveloping function. This is straight forward if $c \geq 3$, but the case when $c \in (2, 3)$ requires an extra argument.

3.8 Enveloping 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

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

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 eventuslly 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. We note that with $\alpha = -1$, $\phi(x)$ would have a pole at $1/3$ and could be used to show that $x = 1$ is globally stable for all $x > 1/3$.

This $f(x)$ is *not* locally stable because for small $\epsilon > 0$, if $x_0 = 1 - \epsilon$ then $x_1 = 1 + 4\epsilon$ and this iterate is not in the same ϵ neighborhood of 1 as the initial point.

4 Conclusion 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.

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 [1, 4] has drawings of such curves. 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 than those we used as examples.

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. For example, Model II is a second degree polynomial, but even a third degree polynomial would have local stability implying global stability. Singer[18] notes that this follows from the Schwarzian condition. It also follows from our doubly positive theorem. Cull[4] shows that a slight generalization of Model I also has local stability implies global stability, and he gives examples of generalizations which do **not** have local implies global.

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