Methods of Analysis. III. Stability

What happens to a point very near an equilibrium?

If points near an equilibrium tend to move towards the equilibrium over time, the equilibrium is said to be **locally stable**.

If points near an equilibrium tend to move away from the equilibrium over time, the equilibrium is said to be **locally unstable**.

> By definition, when we say that an equilibrium point $\hat{n}$ is locally stable, we mean that all solutions which begin from an initial condition close to $\hat{n}$ converge to $\hat{n}$ as time goes to infinity.
>
> -- Roughgarden p.557

An equilibrium point is said to be **globally stable** if all initial starting conditions lead to it.

Goal: To determine whether a small perturbation away from an equilibrium point will grow or shrink in magnitude over time.

Methods of Analysis. III. Stability

Mathematical Aside: Taylor Series

Most nicely behaved functions, **f(x)**, can be rewritten as:

$$f(x) = \sum_{k=0}^{\infty} \frac{f^{(k)}(a)}{k!} (x-a)^k$$

where $f^{(k)}(a)$ is the kth derivative of the function with respect to **x** evaluated at the point **a**. (This is proven in many calculus books.)

How does this help?

If we have an equilibrium point, call it **a**, and we have a starting condition **x** which is near **a**, then we can use the Taylor Series to rewrite the equations that describe how the system changes over time.

If we start near enough to the equilibrium, $(\mathbf{x}-\mathbf{a})^{\mathbf{k}}$ will be tiny for **k** greater than one and the function will be dominated by the first two terms in the sum with **k=0** and **k=1**:

$$f(x) \approx f(a) + f'(a)\,(x-a)$$

This is great! No matter how complicated and non-linear an equation we have, we can get an approximate equation that describes the dynamics near an equilibrium point. This approximate equation is linear in **x** and can be easily analysed.

Stability analysis in discrete one-variable models

Given a recursion equation in one variable ($x[t+1] = f(x)$) with an equilibrium $\hat{x}$, when will a small perturbation (ε) away from the equilibrium grow in magnitude over time?

At time t, say that the population is a small distance from the equilibrium: $\hat{x} + \varepsilon[t]$. (Note that $\varepsilon[t]$ might be negative.)

At time t+1, the population will be at $\hat{x} + \varepsilon[t+1]$, which equals $f(\hat{x} + \varepsilon[t])$.

Using the Taylor Series of this function:

$$\hat{x} + \varepsilon[t+1] = f(\hat{x} + \varepsilon[t])$$
$$\approx f(\hat{x}) + f'(\hat{x})\,(\hat{x} + \varepsilon[t] - \hat{x}) \quad \text{[Taylor Series around } \hat{x}]$$
$$\approx f(\hat{x}) + f'(\hat{x})\,\varepsilon[t]$$

But we know that $f(\hat{x}) = \hat{x}$, since at equilibrium the system does not change over time.

Therefore

$$\longrightarrow \quad \varepsilon[t+1] \approx f'(\hat{x})\,\varepsilon[t]$$

The perturbation will

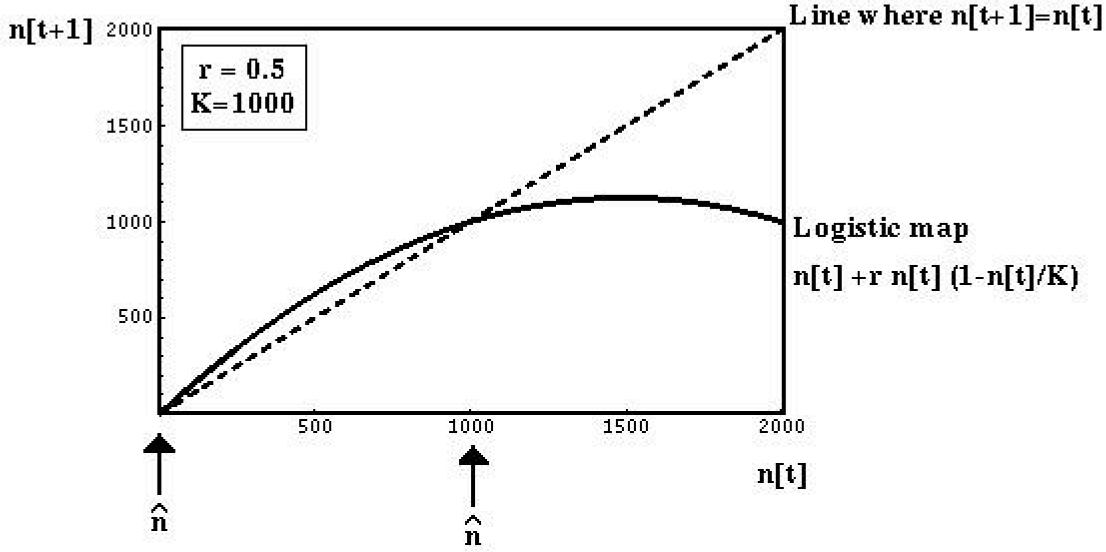
- stay on the same side of the equilibrium if $f'(\hat{x})$ is positive
  - and grow if $f'(\hat{x})$ is greater than one ($\hat{x}$ locally unstable)
  - and shrink if $f'(\hat{x})$ is between zero and one ($\hat{x}$ locally stable)

- move from one side of the equilibrium to the other side of the equilibrium if $f'(\hat{x})$ is negative
  - and grow if $f'(\hat{x})$ is below negative one ($\hat{x}$ locally unstable)
  - and shrink if $f'(\hat{x})$ is between negative one and zero ($\hat{x}$ locally stable)

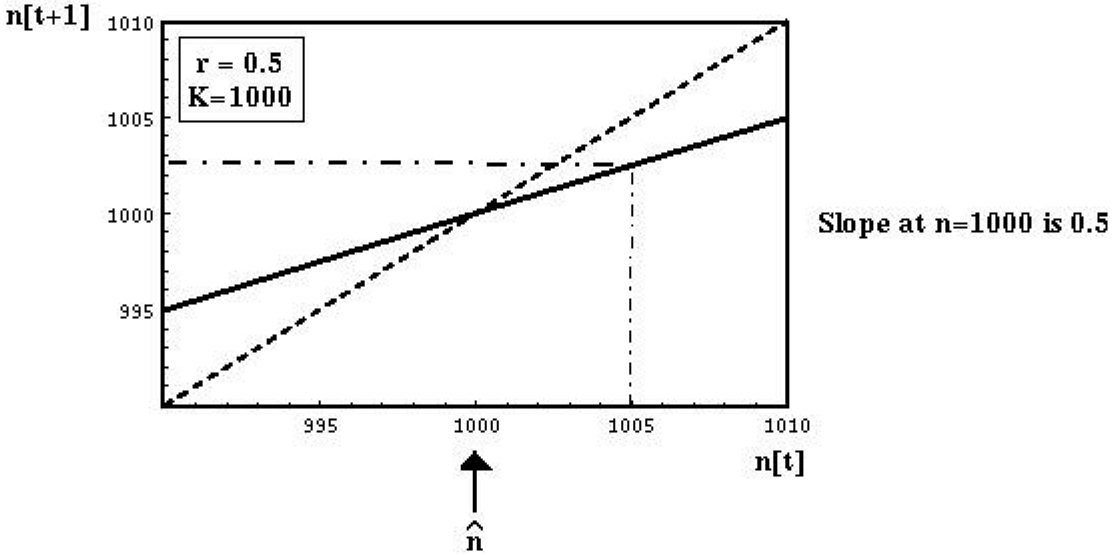
These conditions have a fairly simple graphical interpretation.

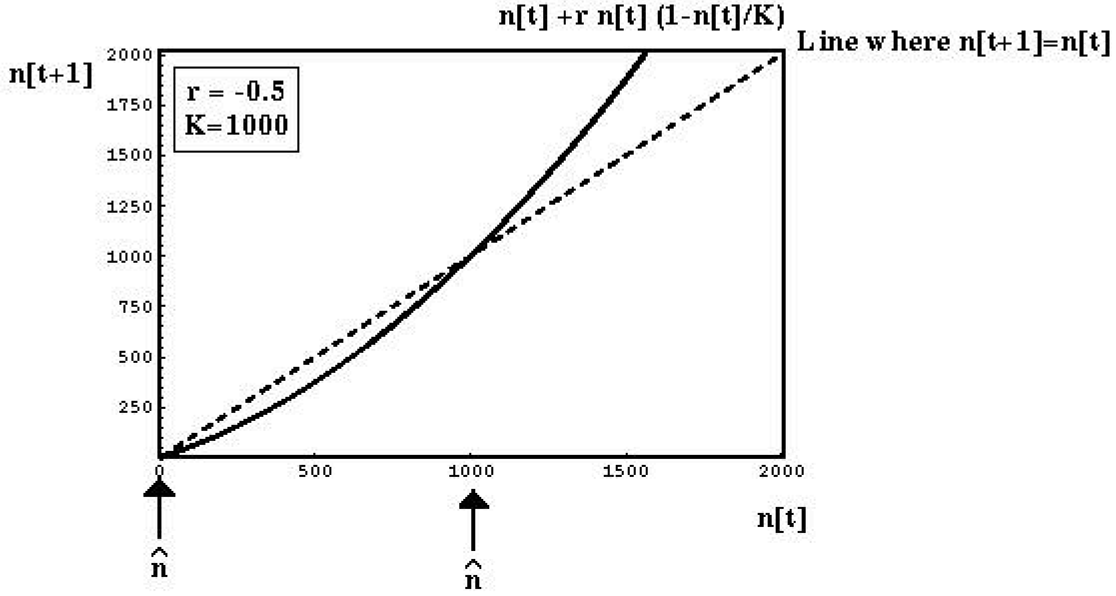
As an example, we'll consider the logistic equation in discrete time, with K=1000 and r=+/-0.5.

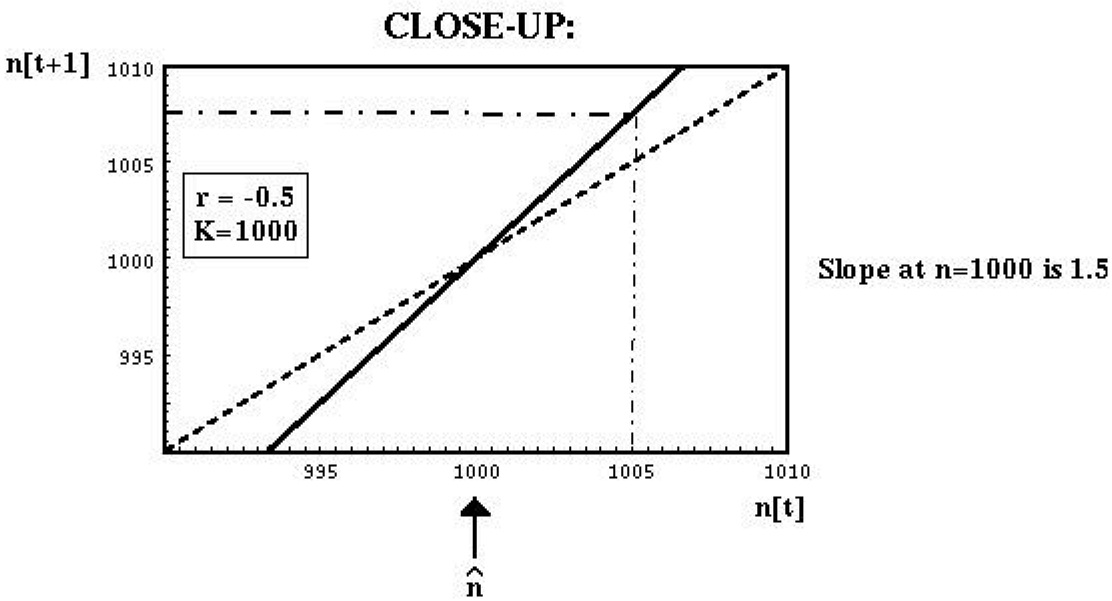
For populations started near carrying capacity (e.g. n[t]=1005), the slope of the recursion equation predicts whether the system will move closer to or further away from the equilibrium.


n[t+1]
Line where n[t+1]=n[t]
r = 0.5
K=1000
Logistic map
n[t] +r n[t] (1-n[t]/K)
n[t]
2000
1500
1000
500
500
1000
1500
2000
n̂
n̂

CLOSE-UP:


n[t+1]
r = 0.5
K=1000
Slope at n=1000 is 0.5
n[t]
1010
1005
1000
995
995
1000
1005
1010
n̂





Stability analysis in continuous one-variable models

Again we focus on a small perturbation (ε) away from an equilibrium ($\hat{x}$) and determine whether this perturbation will grow or shrink.

If at time t the population is a small distance from equilibrium: $\hat{x} + \varepsilon[t]$, the rate of change in x will be $dx/dt = d(\hat{x} + \varepsilon[t])/dt$.

In this case, dx/dt is the function that we wish to approximate using the Taylor Series:

$$\frac{d(\hat{x} + \varepsilon[t])}{dt} = f(\hat{x} + \varepsilon[t])$$

$$\approx f(\hat{x}) + f'(\hat{x})\,(\hat{x} + \varepsilon[t] - \hat{x}) \quad \text{[Taylor Series around } \hat{x}\text{]}$$

$$\approx f(\hat{x}) + f'(\hat{x})\,\varepsilon[t]$$

Now, $f(\hat{x})$ equals zero, since dx/dt = 0 at equilibrium.

Furthermore, by the linearity property of derivatives:

$$\frac{d(\hat{x} + \varepsilon[t])}{dt} = \frac{d\hat{x}}{dt} + \frac{d\varepsilon[t]}{dt} = \frac{d\varepsilon[t]}{dt}$$

Therefore, the perturbation will change over time at a rate

$$\longrightarrow \quad \frac{d\varepsilon[t]}{dt} \approx f'(\hat{x})\,\varepsilon[t]$$

The perturbation will

- grow if $f'(\hat{x})$ is positive ($\hat{x}$ locally unstable),
- shrink if $f'(\hat{x})$ is negative ($\hat{x}$ locally stable).

Exponential Growth Model

Discrete Model

Let f(n) = n[t+1] = R n[t] and note that the only equilibrium is $\hat{n}$ = 0.

For the stability analysis in discrete time we must find $f'(\hat{n})$.

f'(n) = d(R n)/dn = R

$f'(\hat{n})$ therefore equals R.

- If R < 1, a perturbation near $\hat{n}$ will shrink ($\hat{n}$=0 is locally stable).
- If R > 1, a perturbation near $\hat{n}$ will grow ($\hat{n}$=0 is locally unstable).

Makes sense: Individuals have to have more than one offspring on average for the population to grow when it is very small.

Continuous Model

Now let f(n) = dn/dt = r n. Again the only equilibrium is $\hat{n}$ = 0.

For the stability analysis in continuouus time we must find $f'(\hat{n})$.

$$f'(n) = d(r\,n)/dn = r$$

$f'(\hat{n})$ therefore equals r.

- If r < 0, a perturbation near $\hat{n}$ will shrink ($\hat{n}$=0 is locally stable).
- If r > 0, a perturbation near $\hat{n}$ will grow ($\hat{n}$=0 is locally unstable).

Makes sense: Individuals have to have a positive rate of reproduction for the population to grow when it is very small.

Haploid Selection Model (Discrete)

For the one-locus selection model, the recursion function is:

$$f(p) = \frac{p\ W_A}{p\,W_A + (1-p)\,W_a}$$

To perform a Taylor Series analysis, we first must find the derivative of f with respect to p:

$$f'(p) = \frac{W_A\, W_a}{(p\, W_A + (1-p)\, W_a)^2}$$

The first equilibrium of the haploid model is $\hat{p}$=0. At this equilibrium,

$$f'(0) = \frac{W_A}{W_a}$$

Therefore, if we start at some point near 0, say $\varepsilon[t]$, then in the next generation the allele frequency will be approximately $\varepsilon[t]\, W_A/W_a$.

The allele frequency will move towards zero if $W_A < W_a$ ($\hat{p}$=0 is locally stable).

The allele frequency will move away from zero if $W_A > W_a$ ($\hat{p}$=0 is locally unstable).

Haploid Selection Model (Discrete)

The other equilibrium in the haploid model is $\hat{p}$=1. The derivative of the recursion function at this equilibrium is:

$$f'(1) = \frac{W_a}{W_A}$$

Therefore, if we start at some point near 1, say $1-\varepsilon[t]$, then in the next generation the allele frequency will be approximately $1-\varepsilon[t]\, W_a/W_A$.

The allele frequency will move towards one if $W_A > W_a$ ($\hat{p}$=1 is locally stable).

The allele frequency will move away from one if $W_A < W_a$ ($\hat{p}$=1 is locally unstable).

Haploid Selection Model (Continuous)

A similar analysis can be performed using the continuous model. Now our function is **dp/dt**:

$$f(p) = (r_A - r_a)\,p\,(1-p)$$

What will f'(p) equal?

There are two equilibria in this model, $\hat{p}$=0 and $\hat{p}$=1.

What will f'(0) equal?

When will $\hat{p}$=0 be stable?

When will $\hat{p}$=0 be unstable?

What will f'(1) equal?

When will $\hat{p}$=1 be stable?

When will $\hat{p}$=1 be unstable?

When A is favored, the population moves toward fixation on A and away from fixation on a (and vice versa).

Diploid Selection Model (Discrete)

We have to evaluate **f'($\hat{p}$)** for each of the three equilibria of the diploid model, using the function, **f(p)**, given by the recursion equation for the diploid selection model:

$$f(p) = \frac{p^2 W_{AA} + p\,q\,W_{Aa}}{p^2 W_{AA} + 2\,p\,q\,W_{Aa} + q^2 W_{aa}}$$

$$\downarrow$$

	$\hat{p} = 0$	$\hat{p} = \dfrac{WAa - Waa}{2WAa - WAA - Waa}$	$\hat{p} = 1$
$f'(\hat{p}) =$	$\dfrac{WAa}{Waa}$	$\dfrac{WAA\,(WAa - Waa) + Waa\,(WAa - WAA)}{WAa^2 - WAA\,Waa}$	$\dfrac{WAa}{WAA}$

Results:

- Perturbations near $\hat{p}$**=0** grow if $\mathbf{W_{Aa}} > \mathbf{W_{aa}}$ but shrink if $\mathbf{W_{Aa}} < \mathbf{W_{aa}}$.
- Perturbation near $\hat{p}$**=1** grow if $\mathbf{W_{Aa}} > \mathbf{W_{AA}}$ but shrink if $\mathbf{W_{Aa}} < \mathbf{W_{AA}}$.

How about the polymorphic equilibrium?

How Mathematica Can Make Life Easier

```
pprime := (p^2*WAA+p*(1-p)*WAa)/
          (p^2*WAA+2*p*(1-p)*WAa+(1-p)^2*Waa)
```

```
Factor[
D[pprime,p]/.
p->0]
```

$$\frac{WAa}{Waa}$$

```
Factor[
D[pprime,p]/.
p->1]
```

$$\frac{WAa}{WAA}$$

```
Factor[
D[pprime,p]/.
p->(WAa-Waa)/(2*WAa-WAA-Waa)]
```

$$\frac{-(Waa\ WAa) + 2\ Waa\ WAA - WAa\ WAA}{-WAa^2 + Waa\ WAA}$$

```
Factor[%-1]
```

$$\frac{(Waa - WAa)\ (-WAa + WAA)}{-WAa^2 + Waa\ WAA}$$

Diploid Selection Model (Discrete)

We can rewrite $\mathbf{f'(\hat{p})}$ as

$$1 - \frac{(WAa-Waa)(WAa-WAA)}{WAa^2 - WAA\ Waa}$$

We need only look at the cases where the polymorphic equilibrium is valid (lies between 0 and 1):

- If $\mathbf{W_{AA} < W_{Aa} > W_{aa}}$, a perturbation near $\hat{p}$ will shrink (the internal polymorphic state is locally stable).

- If $\mathbf{W_{AA} > W_{Aa} < W_{aa}}$, a perturbation near $\hat{p}$ will grow (the internal polymorphic state is locally unstable).

To summarize:

- $\mathbf{W_{AA} > W_{Aa} > W_{aa}}$ (Directional selection favoring A)
  - Fixation on A is locally stable
  - Fixation on a is locally unstable
  - Polymorphic equilibrium is not valid.
- $\mathbf{W_{AA} < W_{Aa} < W_{aa}}$ (Directional selection favoring a)
  - Fixation on A is locally unstable
  - Fixation on a is locally stable
  - Polymorphic equilibrium is not valid.
- $\mathbf{W_{AA} < W_{Aa} > W_{aa}}$ (Heterozygote advantage or overdominance)
  - Fixation on A is locally unstable
  - Fixation on a is locally unstable
  - Polymorphic equilibrium is locally stable.
- $\mathbf{W_{AA} > W_{Aa} < W_{aa}}$ (Heterozygote disadvantage or underdominance)
  - Fixation on A is locally stable
  - Fixation on a is locally stable
  - Polymorphic equilibrium is locally unstable.

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