Population Dynamics

II. Non-Linear Models

Linear models of population dynamics are not very realistic in at least one crucial aspect: the population either grow forever or go extinct.. Stability is attained only is very special conditions which are unlikely to be satisfied. If we go back to eq. (I.1)

$$P_{n+1} = r P_n$$

we can try to fix this problem by limiting the growth rate r is the population gets too large. One way to do that is setting

$$P_{n+1} = \frac{K P_n}{b + P_n} \qquad (1)$$

$$\simeq \begin{cases} \frac{K}{b} P_n & \text{if} \quad P_n << b \\ K & \text{if} \quad P_n >> b \end{cases}$$

Therefore K/b plays the role of r at small populations, but the population saturates at K, which is the "carrying capacity" of the region. This is much more satisfying but the equation has become non-linear. We cannot solve it and write P_n as a function of P_0 as before.

Because a complete solution of a non-linear equation is not generally possible we adopt a different strategy. Let

$$X_{n+1} = f(X_n) \tag{2}$$

represent a generic non-linear equation for the population X. Here is what we do:

1) Look for equilibrium solutions. These are special values of X such that $f(X)$ produces X again: the population remains constant in time

The equation to solve is

$$x = f(x)$$

2) Study the dynamic in the vicinity of this solutions. If $\bar{x}_i = f(\bar{x}_i)$ we consider

$$x_n = \bar{x}_i + \delta x_n \qquad (3)$$

where δx_n is a small deviation from $\bar{x}_i$ at generation n. What is the population at $n+1$? If δx_n is small we expect x_{n+1} to be still close to $\bar{x}$:

$$x_{n+1} = \bar{x} + \delta x_{n+1} \qquad (4)$$

If $|\delta x_{n+1}| > |\delta x_n|$ the dynamic is pushing the population away from the equilibrium and $\bar{x}$ is an <u>UNSTABLE EQUILIBRIUM</u>. If $|\delta x_{n+1}| < |\delta x_n|$ the dynamic is moving the population back towards $\bar{x}$, and the point is <u>STABLE</u>.

Replacing (3) and (4) in (2):

$$\bar{x} + \delta x_{n+1} = f(\bar{x} + \delta x_n)$$

$$\simeq f(\bar{x}) + \delta x_n \frac{\partial f}{\partial x}(\bar{x})$$

$$= \bar{x} + \delta x_n \frac{\partial f}{\partial x}(\bar{x})$$

where we used $f(\bar{x}) = \bar{x}$ and $\frac{\partial f}{\partial x}(\bar{x})$ is the derivative of f evaluated at $\bar{x}$. Therefore

$$\delta x_{n+1} = \delta x_n \frac{\partial f}{\partial x}(\bar{x}) \qquad (5)$$

and we have a simple criterion for the stability of $\bar{x}$:

$$\begin{cases} \bar{x} \text{ is stable if } \left| \frac{\partial f}{\partial x}(\bar{x}) \right| < 1 \\ \bar{x} \text{ is unstable if } \left| \frac{\partial f}{\partial x}(\bar{x}) \right| > 1 \end{cases} \qquad (6)$$

Let us work out the system described by eq. (1). The equilibria are solutions of

$$\bar{p} = \frac{K\bar{p}}{b+\bar{p}}$$

or

$$\bar{p}\,(b+\bar{p}) = K\bar{p}\,.$$

There are two solutions: $\bar{p}_0 = 0$
$\bar{p} = K-b\,.$

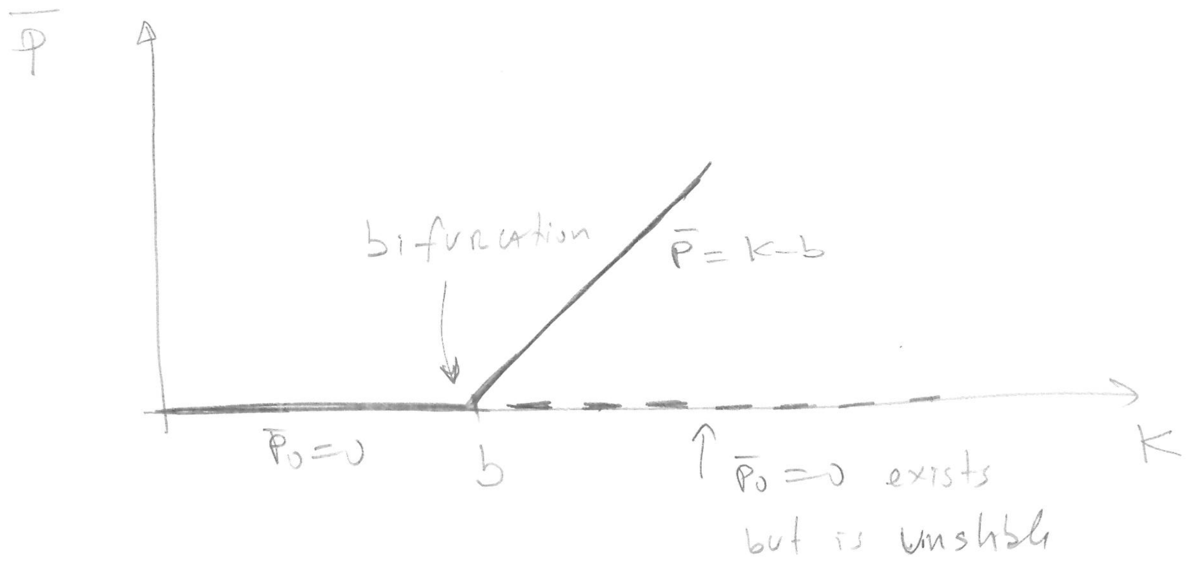
Stability analysis needs $\frac{\partial f}{\partial p}(\bar{p})$ where $f = \frac{Kp}{b+p}$

$$\frac{\partial f}{\partial p} = \frac{K}{b+p} - \frac{Kp}{(b+p)^2} = \frac{Kb}{(b+p)^2}$$

For the equilibrium point $\bar{p}_0 = 0$ $\frac{\partial f}{\partial p}(\bar{p}_0) = K/b\,.$

For $\bar{p} = K-b$ we find $\frac{\partial f}{\partial p}(\bar{p}) = b/K$. Therefore, if $K < b$ extinction is a stable solution and if $K > b$ the population will converge to $\bar{p} = K-b$.

Graphically we have



At $K = b$, exactly when $\frac{\partial f}{\partial P}(\bar{P}) = 1$ the solution $\bar{P} = K - b$ branches off $\bar{P}_0$. This is a bifurcation.

This simple example shows that slightly more complex equations can bring a lot of interesting features to the model:

- the equilibrium solution $\bar{P} = K - b$, for $K > b$, is finite
- it can be controlled by a parameter
- it displays a bifurcation at $K = b$.

THE LOGISTIC EQUATION

The denominator introduced in eq. (1) has the effect of limiting the total population that the region can support. Another way of including this property is by setting

$$P_{n+1} = r P_n \left(1 - P_n / K\right) .$$

Once again the growth rate $r(1 - P_n/K)$ depends on the population and decreases as $P_n \to K$. Defining

$$x_n = P_n / K = \text{population in units of } K$$

we obtain

$$x_{n+1} = r x_n (1 - x_n) . \qquad (7)$$

This equation is known as the logistic equation and has been studied by many people. It has incredibly complicated behavior and was popularized by Robert May. I am going to briefly discuss some of its properties here but the reader can find a lot of material about it on the web.

- equilibrium solutions

Setting $f(x) = rx(1-x) = x$ we find

$\bar{x}_0 = 0$

$\bar{x}_r = 1 - 1/r \Rightarrow$ positive only for $r > 1$

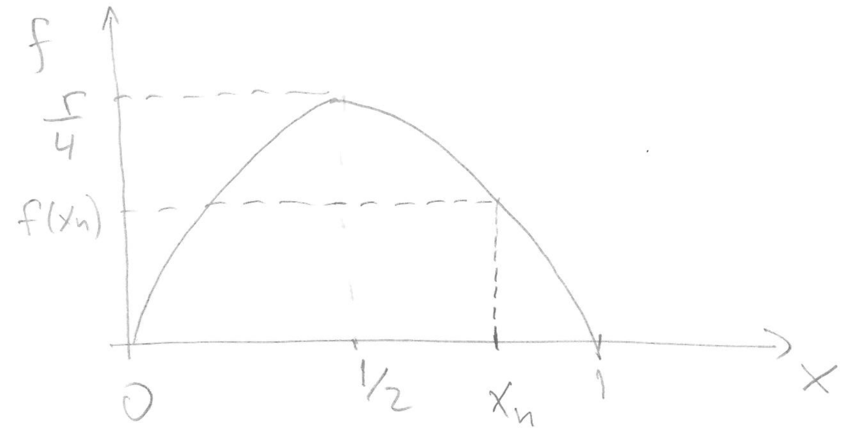
- stability

$$\frac{df}{dx} = r - 2rx \Rightarrow \begin{cases} \text{for } \bar{x}_0 = 0, & \frac{df}{dx} = r \\ \text{for } \bar{x}_r = 1 - \frac{1}{r}, & \frac{df}{dx} = 2 - r \end{cases}$$

Therefore, for $0 < r < 1$ the solution $\bar{x}_0 = 0$ is stable and x_r is unstable. From the biological point of view x_r should not be considered in this interval, since it is negative.

For $1 < r < 3$ $\bar{x}_0$ is unstable, since $\left|\frac{df}{dr}\right| > 1$ and $\bar{x}_r$ is stable. However, if $r > 3$, say $r = 3 + \epsilon$, $2 - r = -1 - \epsilon$ and $\left|\frac{df}{dr}\right| > 1$ for $\bar{x}_r$ as well and the population will no reach an equilibrium! However, as long as $r < 4$, $f(x)$ is always bounded between

0 and 1, and the population oscillates in the interval $0 < x < 1$ or $0 < P < K$:



<u>Exercise</u>: Take $r = 3.3$, $x_0 = 0.5$ and calculate the "orbit" $x_1, x_2, x_3, \ldots$.

<u>Solution</u>

$x_0 = 0.5$

$x_1 = 0.825$

$x_2 = 0.476$

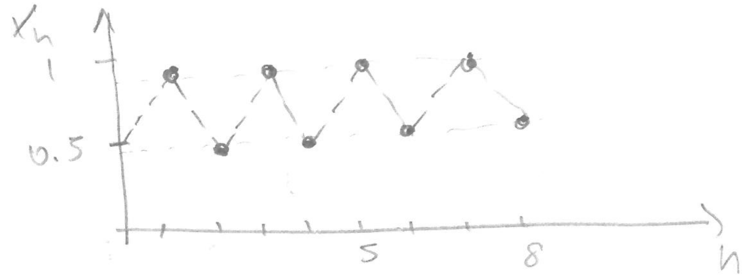
$x_3 = 0.823$

$x_4 = 0.480$

$x_5 = 0.824$

$x_6 = 0.479$

$x_7 = 0.824$



The population clearly oscillates between two values, 0.48 and 0.82. We can find these points explicitly with the following trick:

If there exists two points x_1 and x_2 such that

$$x_2 = f(x_1) \quad \text{and} \quad x_1 = f(x_2)$$

then, applying the dynamics twice returns to same point:

$$x_1 = f(x_2) = f[f(x_1)].$$

Explicitly we obtain

$$f(x) = rx(1-x)$$

$$f(f(x)) = rf(x)(1-f(x)) = r[rx(1-x)][1-rx(1-x)]$$

And we need to solve

$$r^2x(1-x)[1-rx(1-x)] = x. \qquad (8)$$

This is a polynomial of degree 4 and the solutions are

1) $\bar{x}_0 = 0$

2) $\bar{x}_r = 1 - 1/r$ (9)

3) $\bar{x}_\pm = \dfrac{r+1 \pm \sqrt{(r-3)(r+1)}}{2r}$

Solution $X_\pm$ are the ones we are looking for. It can be checked that

$$f(X_\pm) = X_\mp$$

and that they are real only for $r > 3$. Are these equilibria of the "two-steps equation" stable? To figure this out we need to calculate

$$\lambda \equiv \frac{d}{dx}\left[f(f(x))\right]\Big|_{X_\pm} = \frac{df}{dx}(f(x))\,\frac{df}{dx}(x)$$

$$= \frac{df}{dx}(X_+)\,\frac{df}{dx}(X_-) \qquad (10)$$

(if $x = X_+$, $f(x) = X_-$ and vice-versa). We get

$$\lambda = (r - 2rX_+)(r - 2rX_-) = 1 - (r-3)(r+1) \,. \qquad (11)$$

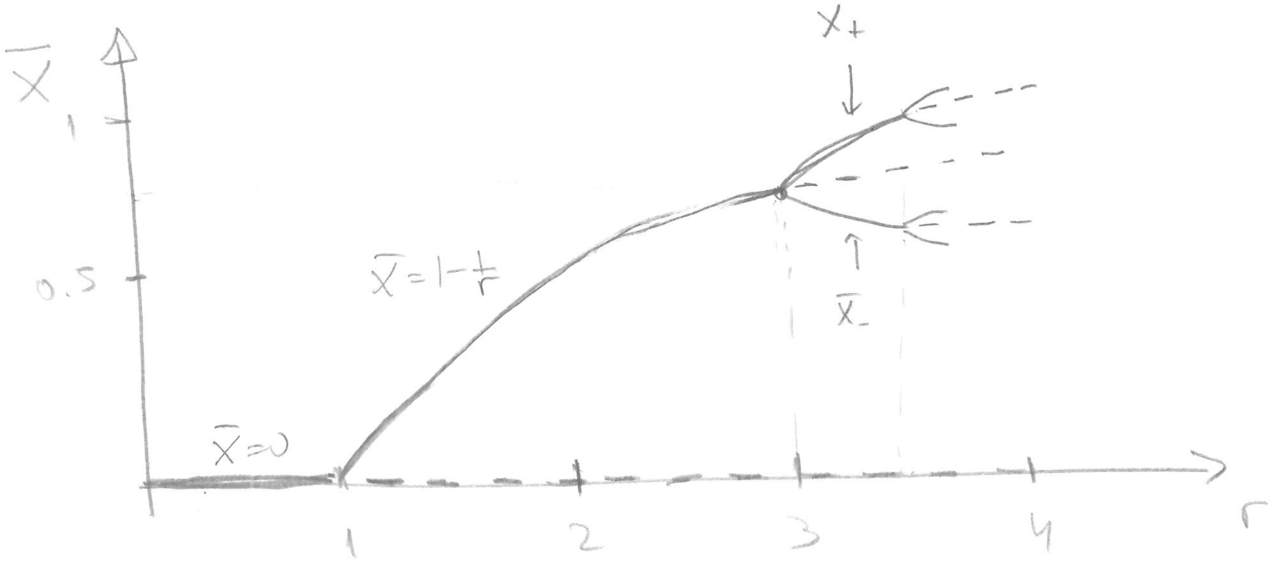
For $r = 3.3$ we find $\lambda = -0.29$, which shows that this "period two" oscillation is stable. For $r = 3.5$ we obtain $\lambda = -1.25$ which indicates instability. To find out exactly the critical r we se

$$1 - (r-3)(r+1) = -1$$

and find

$$r = 1 + \sqrt{6} \approx 3.4495$$

The bifurcation diagram, similar to that on page 6, becomes



After $r=1+\sqrt{6}$ the population oscillates between four values and then bifurcates again to an 8-points solutions and so on. Very soon a cascade of bifurcations take place and the dynamics become very complicated. For more see Robert Devaney, An Introduction to Chaotic Dynamical Systems.

Exercises: Solve eq (8) and demonstrate (10) and (11).

Systems of Non-Linear Equations

Consider two populations, like prey and predator, or plants and pollinators, whose dynamics is given by

$$x_{n+1} = f(x_n, y_n) \qquad (12)$$
$$y_{n+1} = g(x_n, y_n) \quad .$$

Here the functions f and g describe the interactions between the two species. The equation are usually very hard (or impossible) to solve and we follow the idea of finding the equilibria and study their stability.

Equilibrium points are solutions of the equations

$$\bar{x} = f(\bar{x}, \bar{y}) \qquad (13)$$
$$\bar{y} = g(\bar{x}, \bar{y})$$

To study its stability we consider small deviations and write

$$x_n = \bar{x} + x_n'$$
$$y_n = \bar{y} + y_n'$$

And also write

$$x_{n+1} = \bar{x} + x'_{n+1}$$

$$y_{n+1} = \bar{y} + y'_{n+1} .$$

We obtain

$$\bar{x} + x'_{n+1} = f(x_n + x'_n, y_n + y'_n)$$

$$\bar{y} + y'_{n+1} = g(x_n + x'_n, y_n + y'_n) .$$

Expanding the functions f and g to first order around $(\bar{x}, \bar{y})$ and using (13) we find

$$x'_{n+1} = a_{11} x'_n + a_{12} y'_n \qquad (14)$$

$$y'_{n+1} = a_{21} x'_n + a_{22} y'_n$$

with

$$a_{11} = \frac{\partial f}{\partial x}(\bar{x}, \bar{y})$$

$$a_{12} = \frac{\partial f}{\partial y}(\bar{x}, \bar{y})$$

$$a_{21} = \frac{\partial g}{\partial x}(\bar{x}, \bar{y})$$

$$a_{22} = \frac{\partial g}{\partial y}(\bar{x}, \bar{y})$$

In matrix form

$$W_{n+1} = A\, W_n$$

with $W_n = \begin{pmatrix} x_n \\ y_n \end{pmatrix}$, $A = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}$.

This is exactly the type of linear system we discussed in pages 9–15. Stability is determined by the eigenvalues

$$\lambda_\pm = \frac{\beta}{2} \pm \frac{1}{2}\sqrt{\beta^2 - 4\gamma}$$

$$\beta = a_{11} + a_{22}$$
$$\gamma = a_{11} a_{22} - a_{12} a_{21}$$

When is the solution $(\bar{x}, \bar{y})$ stable ?

(I) If $4\gamma > \beta^2$ $\lambda_\pm$ are complex and can be written as $\lambda_\pm = r e^{\pm i\varphi}$ with $r = \sqrt{\gamma}$.
Therefore $|\lambda_\pm| < 1$ if $\gamma < 1$. (see pg. I-14)

(II) If $4\gamma < \beta^2$ $\lambda_\pm$ are real.

(A) If $\beta > 0$ $\lambda_+ > \lambda_- > 0$ and λ_+ is the "dominant eigenvalue". Stability requires

$\lambda_+ < 1$:

$$\frac{\beta}{2} + \frac{1}{2}\sqrt{\beta^2 - 4\gamma} < 1$$

(A1) $\beta < 2$, otherwise $\lambda_+ > 1$

(A2) $\beta + \sqrt{\beta^2-4\gamma} < 2 \Rightarrow \beta - 2 > \sqrt{\beta^2 - 4\gamma}$

or $\beta^2 - 4\gamma < \beta^2 - 4\beta + 4 \Rightarrow \gamma > \beta - 1$

(A3) $4\gamma < \beta^2 < 4 \Rightarrow \gamma < 1$

Putting all together we see that the condition (for $\beta > 0$) is

$$\beta - 1 < \gamma < 1 \quad \text{or} \quad \beta < \gamma + 1 < 2$$

(B) If $\beta < 0$ $\lambda_- < \lambda_+ < 0$ and we need $\lambda_- > -1$. We obtain

$$\boxed{|\beta| < \gamma + 1 < 2}$$

which holds also for $\beta > 0$ and is the condition for stability.

Examples

(1) Host – Parasitoid equations

$$H_{n+1} = F H_n \left(1 + \frac{a P_n}{k}\right)^{-k}$$

$$P_{n+1} = H_n \left[1 - \left(1 - \frac{a P_n}{k}\right)^{-k}\right]$$

where $H_n(1 + aP_n/k)^{-k}$ is the fraction of hosts surviving the parasitism. Re-writing

$$P_{n+1} = H_n - H_{n+1}/F$$

Equilibrium solutions are

$$(\bar{H}, \bar{P}) = (0, 0) \longrightarrow \text{stable if } F<1$$

or

$$\begin{cases} \bar{H} = \left(\dfrac{F}{F-1}\right) \dfrac{k}{a} \left(F^{1/k} - 1\right) \\[2ex] \bar{P} = \dfrac{k}{a}\left(F^{1/k} - 1\right) \end{cases}$$

For this point we find

$$\beta = 1 + \frac{k}{F-1} \, \frac{F^{1/k} - 1}{F^{1/k}}$$

$$\gamma = k \left(\frac{F^{1/k} - 1}{F^{1/k}}\right)\left(\frac{F}{F-1}\right).$$

(2) Plant – Herbivores

$$v_{n+1} = f\, v_n\, e^{-a h_n}$$
$$h_{n+1} = r\, h_n \left(\delta - \frac{h_n}{v_n} \right)$$

$f, r, \delta, a > 0$.

(A) Show that $\bar{v} = \dfrac{r\bar{h}}{r\delta - 1}$; $\bar{h} = \dfrac{\ln f}{a}$ is

an equilibrium solution.

(B) Define $V_n = v_n / \bar{v}$, $H_n = h_n / \bar{h}$ and show that the equations become

$$V_{n+1} = V_n\, e^{K(1-H_n)}$$
$$H_{n+1} = b H_n \left[1 + \frac{1}{b} - \frac{H_n}{V_n} \right]$$

where $K = \ln f$, $b = r\delta - 1$.

(C) Draw a diagram in the $b \times K$ plane showing the regions where the equilibrium point $\bar{H} = \bar{V} = 1$ are stable.

(3) Competion for the same resources between two species:

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1 + \alpha N_2}{K_1}\right)$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2 + \beta N_1}{K_2}\right)$$

α, β are degrees of interference of one species on the other.

(4) Intraguild Predation = N_1 and N_2 compete for the same resources and N_1 predates N_2

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1 + \alpha N_2}{K_1}\right) + \gamma N_1 N_2$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2 + \beta N_1}{K_2}\right) - \delta N_1 N_2$$

(5) Epidemics – the SIR model

S = susceptible individuals

I – infected individuals

R = recovered

$$\frac{dS}{dt} = -\beta I S$$

$$\frac{dI}{dt} = \beta I S - \nu I \qquad \Rightarrow \qquad S + I + R = N = \text{const.}$$

$$\frac{dR}{dt} = \nu I$$

(6) Epidemic with incubation period

E = exposed (infected but no infectious)

μ = birth rate $\equiv$ death rate

a^{-1} = incubation period

$$\frac{dS}{dt} = \mu N - \mu S - \beta I S / N$$

$$\frac{dE}{dt} = \beta \frac{IS}{N} - (\mu + a) E$$

$$\frac{dI}{dt} = a E - (\nu + \mu) I \qquad N = S + E + I + R = \text{const.}$$

$$\frac{dR}{dt} = \nu I - \mu R$$

(7) The quasi-species equation

Consider n "species" specified by n genomes $g_1, g_2, \ldots g_n$. The frequency of genome i is x_i and

$$\frac{dx_i}{dt} = \sum_{j=1}^{n} x_j f_j q_{ji} - \phi x_i$$

where

f_i = fitness (reproductive rate) of species i

q_{ji} = mutation probability from j to i

ϕ = average fitness of the population

$$= \sum_{i=1}^{n} f_i x_i$$

– SHOW THAT THIS EQUATION IS CONSISTENT with $\sum_{i=1}^{N} x_i = 1$.

(8) The replicator equation

similarly to the previous example,

$$\dot{x}_i = x_i \left[f_i(x) - \phi \right]$$

$$f_i(x) = \sum a_{ij} x_j$$

The fitness of species i is a function of the density of each species.

(9) The replicator-mutator equation

$$\dot{x}_i = \sum_j x_j f_j(x)\, q_{ji} - \phi x_i$$