

Math 345 Intro to Math Biology  
Lecture 7: Models of System of Nonlinear  
Difference Equations

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# Equilibrium

**Model:**  $x_{n+1} = f(x_n)$ , here  $f$  is a nonlinear function.

**Equilibrium:** (fixed point, constant solution)

If  $x$  satisfies  $x = f(x)$ , then  $x$  is an equilibrium of the difference equation  $x_{n+1} = f(x_n)$ . An equilibrium is where the graphs of  $y = x$  and  $y = f(x)$  intersect.

**Stability of an equilibrium:** Suppose that  $x_*$  is an equilibrium of  $x_{n+1} = f(x_n)$ . If we start the iteration sequence from any initial point  $x_0$  close to  $x_*$ , we always have  $\lim_{n \rightarrow \infty} x_n = x_*$ , then  $x_*$  is *stable*; otherwise it is unstable.

**Linearization:**

$$f(x) \approx f(x_*) + f'(x_*)(x - x_*)$$

(linear approximation, first order Taylor expansion)

(**IF**  $x$  is close to  $x_*$ )

So near an equilibrium  $x_*$ ,

$$x_{n+1} = f(x_n) \approx f(x_*) + f'(x_*)(x_n - x_*) = x_* + f'(x_*)(x_n - x_*)$$

or  $x_{n+1} - x_* \approx f'(x_*)(x_n - x_*)$  (A linear equation !)

Let  $y_n = x_n - x_*$ . Then  $y_{n+1} = f'(x_*)y_n$ .

If  $f'(x_*) > 1$ , then exponential growth (unstable)

If  $0 < f'(x_*) < 1$ , then exponential decay (stable)

If  $-1 < f'(x_*) < 0$ , then exponential decaying oscillation (stable)

If  $f'(x_*) < -1$ , then exponential growing oscillation (unstable)

# Stability of Equilibrium

**Condition for stability:** Suppose that  $x_*$  is an equilibrium of  $x_{n+1} = f(x_n)$ . Then  $x_*$  is a stable equilibrium if and only if  $|f'(x_*)| < 1$  or  $-1 < f'(x_*) < 1$ , and it is unstable if  $|f'(x_*)| > 1$ .

**Bifurcation:** a qualitative change in the mathematical system, and it can be reflected from the asymptotic behavior of solutions

1. Number of equilibrium changes
2. Stability of equilibria changes (so  $|f'(x_*)| = 1$  at a bifurcation point)

Bifurcation diagram of  $x_{n+1} = f(x_n, \lambda)$ :

the curve of equilibria in  $(\lambda, x)$  space.

Use solid curve for stable equilibria, and dotted curve for unstable equilibria.

**Periodic solution:** If for some integer  $p$ ,  $x_{n+p} = x_n$  for all  $n$ , then  $\{x_n\}$  is a periodic solution with period  $p$  (or  $p$ -cycle) for  $x_{n+1} = f(x_n)$  with period  $p$ .  
(If  $p = 1$ , then it is equilibrium.)

Period two solution (2-cycle):

$x_1 \mapsto x_2 = f(x_1) (\neq x_1) \mapsto x_3 = f(x_2) = f(f(x_1)) = x_1$   
so  $x_1$  is an equilibrium of the map  $f(f(x))$ !

# Bifurcations

**Equilibrium bifurcation:** occurs when  $f'(x_*) = 1$

1. Transcritical bifurcation: 2 equilibria before and after bifurcation point, 1 equilibrium at the bifurcation point (example:  $x_{n+1} = \frac{\lambda x_n}{1 + x_n}$ ,  $x_* = 0$  at  $\lambda = 1$ )
2. Pitchfork bifurcation: 3 equilibria after bifurcation point, 1 equilibrium before or at the bifurcation point (example:  $x_{n+1} = \frac{\lambda x_n}{1 + x_n^2}$ ,  $x_* = 0$  at  $\lambda = 1$ )
3. Saddle-node (or fold, or blue-sky) bifurcation: 0 equilibrium before bifurcation point, 1 equilibrium at the bifurcation point, and 2 equilibria after bifurcation point (example:  $x_{n+1} = 3x_n - x_n^2 - h$ ,  $x_* = 1$  at  $\lambda = 1$ )

**Flip (Period-doubling) bifurcation:**  $f'(x_*) = -1$  but  $[f(f(x_*))]' = 1$  so that the equilibrium  $x_*$  becomes an unstable one, and a stable period-two solution (2-cycle) emerges from the bifurcation)

before bifurcation: stable pattern is a period-one equilibrium,

after bifurcation: a stable pattern is period-two solution

(Example:  $x_{n+1} = \frac{\lambda x_n}{1 + x_n^b}$ ,  $b > 2$ ,  $x_* = (\lambda - 1)^{1/b}$  at  $\lambda = \frac{b}{b-2}$ )

# Chaos

For a non-monotone function  $f(x)$ , the nonlinear model  $x_{n+1} = f(\lambda, x_n)$  can have chaotic dynamics.

**A typical route to chaos:** there exists an equilibrium  $x_*(\lambda)$ .

1. For  $\lambda < \lambda_1$ ,  $x_*$  is stable. At  $\lambda = \lambda_1$ ,  $f'(x_*) = -1$  so a flip bifurcation occurs and a 2-cycle emerges.
2. For  $\lambda_1 < \lambda < \lambda_2$ , the 2-cycle is stable. At  $\lambda = \lambda_2$ , another flip bifurcation occurs and a 4-cycle emerges.
3. In this pattern, 8-cycle, 16-cycle,  $\dots$ ,  $2^n$ -cycle all occurs when  $\lambda$  increases, and this is a **cascade of period-doubling bifurcations**. But all this happens for  $\lambda$  less than a finite number  $\lambda_*$ . After that number  $\lambda_*$ , the solution is no longer periodic but chaotic.

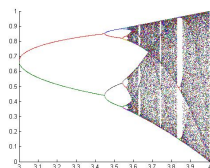
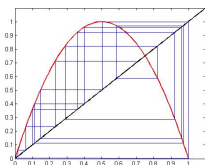
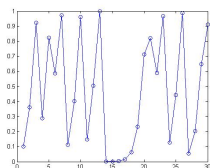
**What is chaos?** The behavior of dynamical systems that are highly sensitive to initial conditions—a response popularly referred to as the “butterfly effect”. It is so called because of the title of a paper given by Edward Lorenz in 1972 to the American Association for the Advancement of Science in Washington, D.C., entitled “*Predictability: Does the Flap of a Butterfly's Wings in Brazil set off a Tornado in Texas?*”. The flapping wing represents a small change in the initial condition of the system, which causes a chain of events leading to large-scale phenomena. Had the butterfly not flapped its wings, the trajectory of the system might have been vastly different.

Example: logistic map  $x_{n+1} = rx_n(1 - x_n)$ , Bellow's model:  $x_{n+1} = \frac{\lambda x_n}{1 + x_n^b}$ ,  $b > 2$ .

# Graphing

Graphing tools: (can be implemented via Matlab or other software)

1. plotting the recursive sequence
2. cobwebbing
3. bifurcation diagram (of chaotic dynamics)



Typical models:

1. Logistic model:  $x_{n+1} = rx_n(1 - x_n)$
2. Bellow's model:  $x_{n+1} = \frac{\lambda x_n}{1 + x_n^b}, b > 0$
3. Ricker's model:  $x_{n+1} = \lambda x_n e^{-kx_n}, k > 0$
4. Hassel's model:  $x_{n+1} = \frac{\lambda x_n}{(1 + x_n)^b}, b > 0$
5. Beverton-Holt model:  $x_{n+1} = \frac{\lambda x_n}{1 + x_n}$

# Two species interactions

## Model:

$$x_{n+1} = f(x_n, y_n, \lambda)$$

$$y_{n+1} = g(x_n, y_n, \lambda)$$

**Equilibrium**  $(x_*, y_*)$ : solve  $x = f(x, y, \lambda)$  and  $y = g(x, y, \lambda)$

## Linearization:

$$\begin{pmatrix} x_{n+1} \\ y_{n+1} \end{pmatrix} = \begin{pmatrix} f_x(x_*, y_*) & f_y(x_*, y_*) \\ g_x(x_*, y_*) & g_y(x_*, y_*) \end{pmatrix} \begin{pmatrix} x_n \\ y_n \end{pmatrix}, \text{ linear matrix model!}$$

**Stability:** If the eigenvalues  $\lambda_1, \lambda_2$  satisfy  $|\lambda_1| < 1$  and  $|\lambda_2| < 1$ , then  $(x_*, y_*)$  is stable, otherwise it is unstable.

**Bifurcation:** occurs when  $|\lambda_i| = 1$ . (transcritical, pitchfork, saddle-node, period-doubling and even more)

Graphing tools: (can be implemented via Matlab or other software)

1. plotting the recursive sequence (same way)
2. cobwebbing (not so good any more)
3. bifurcation diagram (of chaotic dynamics)
4. Phase portrait (graph on  $(x, y)$  plane)

# Host-Parasitoid Model

Parasitoids are insects whose females lay their eggs in or on the bodies of the host insects. Parasitoid eggs develop into parasitoid larvae at the expense of their host. Hosts that have been parasitized thus give rise to the next generation of parasitoids, while only hosts that are not parasitized will give rise to the next generation of hosts.

Let  $H_n$  and  $P_n$  be the number of the hosts and parasitoids, respectively, at generation  $n$ . Further, let  $f(H_n, P_n)$  be the fraction of hosts that are not parasitized. Then

$f(H_n, P_n)H_n$  = number of hosts not parasitized  
 $[1 - f(H_n, P_n)]H_n$  = number of hosts parasitized.

Assuming

1. The host population grows linearly in the absence of the parasitoids, with reproductive rate  $k > 1$ .
2. The average number of eggs laid in a single host that give rise to adult parasitoids is  $c$ .

$$H_{n+1} = kf(H_n, P_n)H_n,$$
$$P_{n+1} = c[1 - f(H_n, P_n)]H_n.$$



# Nicholson-Bailey Model

We assume that encounters between hosts and parasitoids occur at random and are independent (the latter means that parasitoids do not distinguish between hosts that have been parasitized and hosts that have not yet been parasitized). The Law of Mass Action, states that the number of encounters is proportional to the product  $H_n P_n$ , that is,  $aH_n P_n$ , where  $a$  is the constant of proportionality representing the searching efficiency of the parasitoids. The average number of encounters per host is thus  $\nu = aH_n P_n / H_n = aP_n$ . Of course, not all hosts experience this many encounters. Some will experience more, others less.

Let  $p(k)$  be the probability that a host experiences  $k$  encounters. Since we assumed that encounters are random and independent, they are said to follow a Poisson process, and we can use the Poisson distribution for  $p(k) = \frac{\nu^k e^{-\nu}}{k!}$ . Recalling that we defined  $f(H_n, P_n)$  to be the fraction of hosts not parasitized, then  $f(H_n, P_n) = p(0) = e^{-\nu} = e^{-aP_n}$ .

(Nicholson-Bailey 1935)

$$H_{n+1} = kH_n e^{-aP_n},$$

$$P_{n+1} = cH_n [1 - e^{-aP_n}].$$

# Population Genetics Model

A given gene may have one of several forms, called **alleles**. Suppose that there are two alleles, denoted by  $a$  and  $A$ , and that these are passed down in the population from one generation to the next. A given individual could then have one of three combinations (called **genotypes**):  $AA$ ,  $aa$ , or  $aA$ . (The first two combinations are called homozygous, the last one heterozygous.)

A question we might explore is whether the relative frequencies of genes will change, and, if so, whether some new stable distribution will emerge. Until 1914 it was believed that any rare allele would gradually disappear from a population. After a more rigorous treatment of the problem it was shown that if mating is random and all genotypes (combinations of alleles, which in this case are  $AA$ ,  $aa$ , and  $aA$ ) are equally fit (have an equal likelihood of surviving to produce offspring), then gene frequencies do not change. This fact is now known as the **Hardy-Weinberg law**.

## Assumptions:

1. Mating is random.
2. There is no variation in the number of progeny from parents of different genotypes.
3. Progeny have equal fitness (that is, are equally likely to survive).
4. There are no mutations at any step.

# Population Genetics Model

$p$  = frequency of allele  $A$ ,  $q$  = frequency of allele  $a$ , then  $p + q = 1$

$u$  = frequency of  $AA$  genotype,  $v$  = frequency of  $aA$  genotype,  $w$  = frequency of  $aa$  genotype.

$$p = u + \frac{1}{2}v, \quad q = \frac{1}{2}v + w$$

$$u_{n+1} = u_n^2 + u_n v_n + \frac{1}{4}v_n^2$$

$$v_{n+1} = u_n v_n + 2u_n w_n + \frac{1}{2}v_n^2 + v_n w_n$$

$$w_{n+1} = w_n^2 + w_n v_n + \frac{1}{4}v_n^2$$

**Hardy-Weinberg law:**  $p_{n+1} = p_n$  and  $q_{n+1} = q_n$ .