

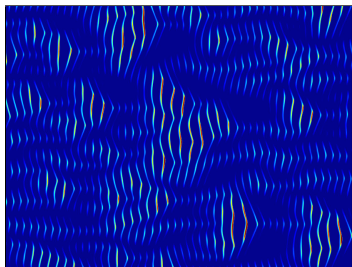
# Ecological Dynamics

## Constructing and analyzing models

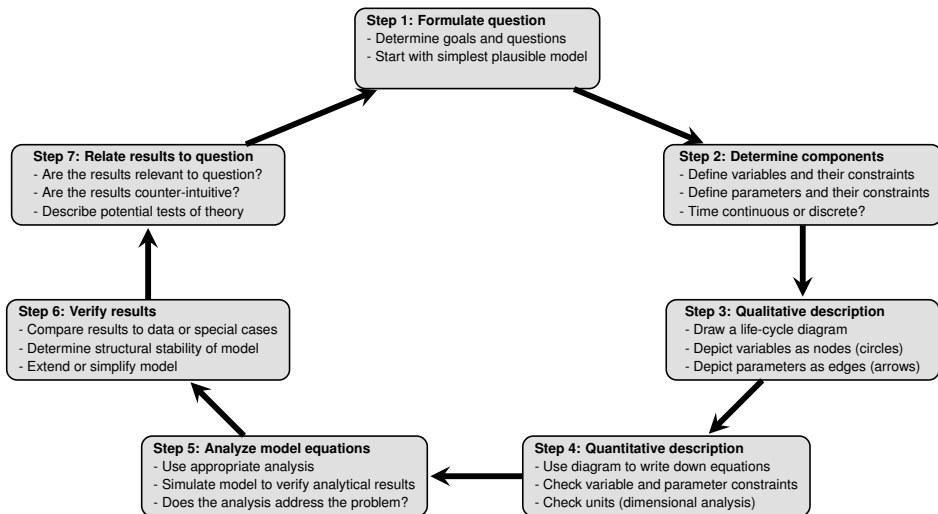
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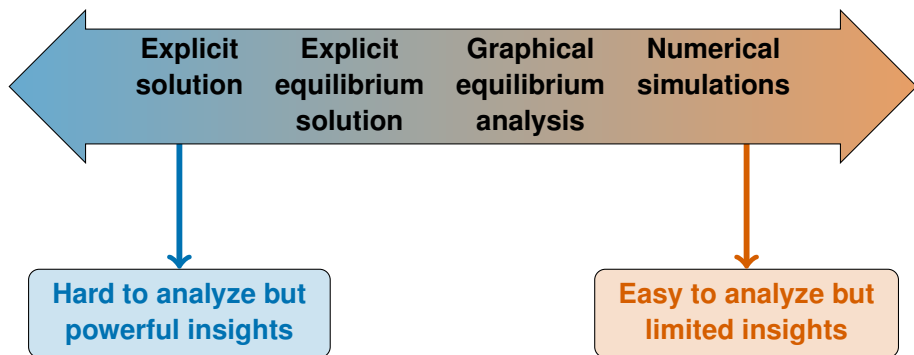
January 22, 2015



# A guide to constructing models (Otto and Day, 2007)



# An overview of model analyses



**Sensitivity analysis** (effect of each parameter on the state variable(s)) and **local stability analysis** (stability of each equilibrium) are often used in conjunction with the approaches above.

## Example of explicit solution

The exponential growth model can be used to predict how the size of a population will change over time in the absence of any resource limitation:

$$\frac{dN}{dt} = rN$$

This **toy model** consists of a single parameter  $r$ , which represents the intrinsic rate of growth (births minus deaths), and a single state variable  $N$ , which represents the size of the population.

**Explicit solutions** (also called **closed-form solutions**) express the state variable(s) as a function of the model parameter(s). The explicit solution for the exponential model is  $N(t) = N_0 e^{rt}$  where  $N_0$  is the initial abundance at time  $t = 0$ .

This expression allows us to understand how changes in  $r$  will affect population size. For instance, we can immediately see that  $0 \leq N(t) < \infty$  which is a **constraint** that the size of a population must satisfy.

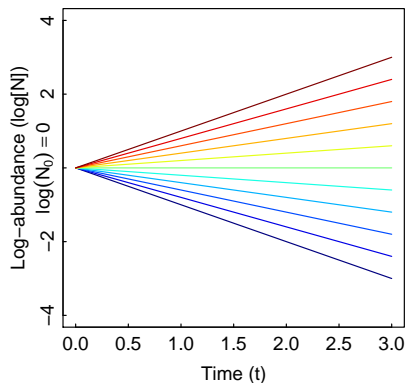
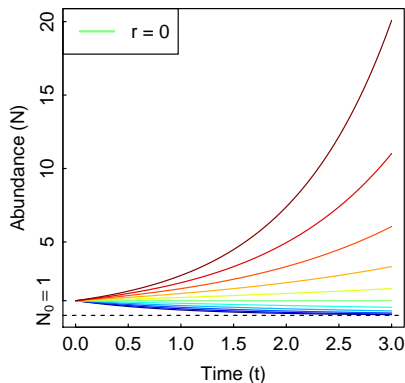
## Example of explicit solution

Although extremely informative, **explicit solutions** can typically only be computed for **linear** or a very limited set of **nonlinear** differential equations.

A differential equation is **linear** if: 
$$\frac{df(c[N_1 + N_2])}{dt} = c \frac{df(N_1)}{dt} + c \frac{df(N_2)}{dt}.$$

How would you determine whether the exponential model is a linear differential equation?

# Example of explicit solution



- **Numerical simulations** of the model can be used to **verify the validity** of our explicit solution
- $r > 0$  (warm colors): exponential growth of population size
- $r < 0$  (cold colors): exponential decay of population size to zero

## Example of explicit equilibrium solution

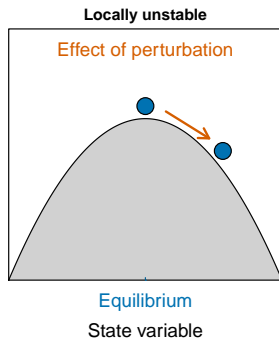
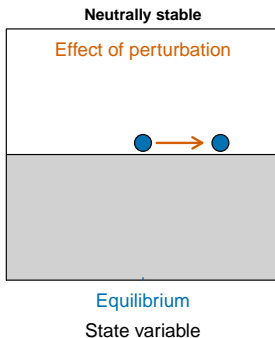
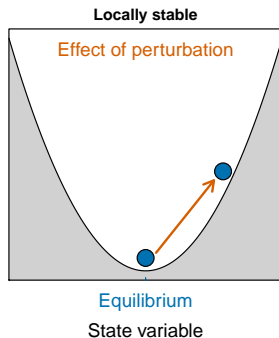
Unfortunately, most biological processes are nonlinear and thus cannot be solved explicitly. However, they can be **solved explicitly at equilibrium**, which is the next best thing. To do so for the exponential model, we set the population growth rate to zero and solve:

$$\frac{dN}{dt} = rN = 0$$

**This equation has two solutions:**  $\hat{N} = 0$  and  $r = 0$ . This means the **trivial equilibrium**  $\hat{N} = 0$  can be achieved if the initial population size  $N_0 = 0$ . A non-trivial equilibrium of  $\hat{N} = N_0$  can be achieved if  $r = 0$ .

**This result makes sense:** a population with zero individuals at the onset will never increase regardless of its intrinsic rate of growth  $r$ . Similarly, a population with  $r = 0$  will not grow or decrease over time, so its equilibrium size  $\hat{N} = N_0$ .

# Local stability analysis of equilibrium solution



Local stability analysis can be used to determine whether a system will return to its equilibrium following an **infinitesimally small perturbation**.

Local stability analysis is typically performed by linearizing around the equilibrium (e.g., via Taylor expansion) but it can also be performed graphically.

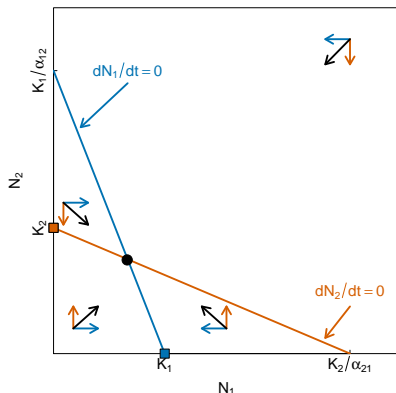


## Example of graphical analysis

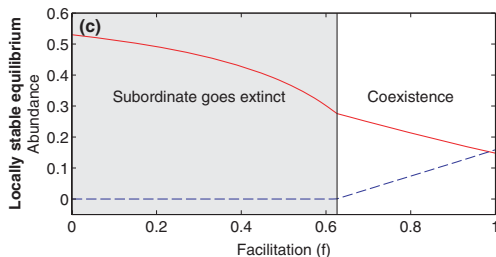
The equilibrium solutions and their local stability are typically analyzed graphically in the Lotka-Volterra competition model:

$$\frac{dN_1}{dt} = r_1 N_1 \left( \frac{K_1 - N_1 - \alpha_{12} N_2}{K_1} \right)$$
$$\frac{dN_2}{dt} = r_2 N_2 \left( \frac{K_2 - N_2 - \alpha_{21} N_1}{K_2} \right)$$

$N_1$  and  $N_2$  are species undergoing logistic growth and competing via coefficients  $\alpha_{12}$  and  $\alpha_{21}$

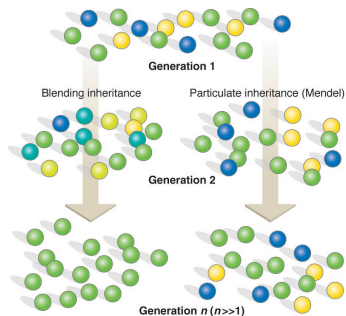


# Numerical simulations



- Complexity can make equilibrium solutions impossible to find explicitly
- For differential equation models where time is continuous, use numerical approaches such as Runge-Kutta methods
- For difference equation models where time is discrete, use for loops to simulate the dynamics
- Simulations are typically run for a range of parameter values and with random initial conditions for the state variables
- The equilibrium values of the state variables are then plotted as a function of the parameter values

# Evolution and the maintenance of genetic variation



- One of the earliest objections to natural selection was that **blending inheritance** of genetic material leads to the loss of genetic variation needed for natural selection to operate
- However, Mendel's work showed that genetic material was transferred from parents to offspring via **particulate inheritance**
- The implications of **particulate inheritance** were discovered via mathematical modeling (Hardy, 1908; Weinberg, 1908)

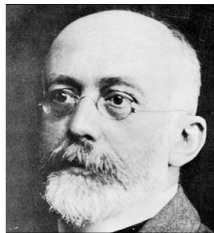
# The Hardy-Weinberg equilibrium

## Definition

In the absence of natural selection, mutation and migration, the allele and genotype frequencies in a population of randomly mating individuals will remain constant over time (Hardy, 1908; Weinberg, 1908)



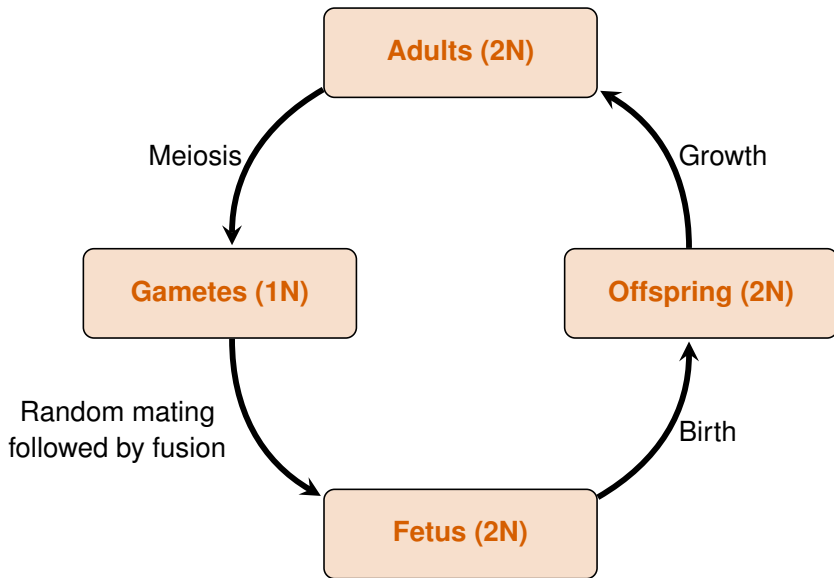
**Godfrey H. Hardy**



**Wilhelm Weinberg**

This remarkable result resolved a major issue in evolutionary biology by showing how genetic variation could be sustained over time and provide the raw material needed for natural selection to operate.

# Diagram of life cycle in diploid organisms



# Deriving the Hardy-Weinberg equilibrium

We assume that individuals mate randomly and that there is no migration, natural selection, or mutation.

The locus in question has two alleles: recessive  $a$  and dominant  $A$ . There are thus four possible outcomes of mating:  $\{AA, aA, Aa, aa\}$ .

Call  $x_0$ ,  $y_0$  and  $z_0$  the respective frequencies of genotypes  $AA$ ,  $Aa$  and  $aa$  at time  $t = 0$  (generation 0); Call  $p_0$  and  $q_0$  the respective frequencies of alleles  $A$  and  $a$  at time  $t = 0$  (generation 0).

Note that  $x_0 + y_0 + z_0 = 1$  and that  $x_0, y_0, z_0 \in [0, 1]$ . Similarly, note that  $p_0 + q_0 = 1$  and that  $p_0, q_0 \in [0, 1]$ .

Now find  $\{x_1, y_1, z_1\}$  and  $\{p_1, q_1\}$  for generation 1.

# Deriving the Hardy-Weinberg equilibrium

Under random mating, the probabilities are independent so for example  $\Pr(AA) = \Pr(A \cap A) = \Pr(A) \cdot \Pr(A) = p_0^2$ . This greatly simplifies the calculation of the genotype and allele frequencies:

Generation 0 mating	Resulting generation 1 genotype
$A \times A$	$x_1 = p_0^2 = (x_0 + y_0/2)^2$
$a \times A$ or $A \times a$	$y_1 = 2p_0q_0 = 2(x_0 + y_0/2) \cdot (z_0 + y_0/2)$
$a \times a$	$z_1 = q_0^2 = (z_0 + y_0/2)^2$
Total (constraint)	$x_1 + y_1 + z_1 = 1$

To verify that  $x_1 + y_1 + z_1 = 1$ , we have to remember that  $p_0 + q_0 = 1$ . Hence,  $x_1 + y_1 + z_1 = p_0^2 + 2p_0q_0 + q_0^2 = (p_0 + q_0)^2 = 1$

We now need to compute the frequencies  $p_1$  and  $q_1$  of alleles  $A$  and  $a$  in generation 1.

# Deriving the Hardy-Weinberg equilibrium

To do so, we note that  $p_1 = x_1 + y_1/2$  and  $q_1 = z_1 + y_1/2$

$$p_1 = x_1 + y_1/2 = p_0^2 + p_0q_0$$

$$q_1 = z_1 + y_1/2 = q_0^2 + p_0q_0$$

Because  $p_0 + q_0 = 1$ , we can replace all instances of  $q_0$  with  $1 - p_0$ :

$$p_1 = p_0^2 + p_0(1 - p_0) = p_0$$

Similarly, we can replace all instances of  $p_0$  with  $1 - q_0$ :

$$q_1 = q_0^2 + q_0(1 - q_0) = q_0$$

The allele frequencies  $\{p, q\}$  reach the equilibrium in one generation. Hence, genetic variation remains constant in the absence of other evolutionary forces. The genotype frequencies  $\{x, y, z\}$  also remain fixed following generation 1.



# References I

- Hardy, G. H. 1908. Mendelian proportions in a mixed population. *Science*, **28**:49–50.
- Otto, S. P. and T. Day. 2007. *A biologist's guide to mathematical modeling in ecology and evolution*. Princeton University Press.
- Weinberg, W. 1908. Über den nachweis der vererbung beim menschen. *Jahreshefte des Vereins für vaterlandische Naturkunde in Württemberg*, **64**:368–382.