

Ecosystem stability

In these lectures we consider models of populations, with an emphasis on the conditions for stability and instability.

Dynamics of a single population

Set

N = population size

r = growth rate

Exponential growth

The simplest possible growth model has N merely growing at rate r :

$$\frac{dN}{dt} = rN, \quad r > 0.$$

The solution predicts *exponential growth*:

$$N(t) = N(0)e^{rt}.$$

Such a model works well when the resource that a population requires for growth is sufficiently abundant.

In cases of such unlimited growth,

$$r = \frac{1}{N} \frac{dN}{dt} = \text{'per capita' or 'specific' growth rate}$$

is constant, independent of N .

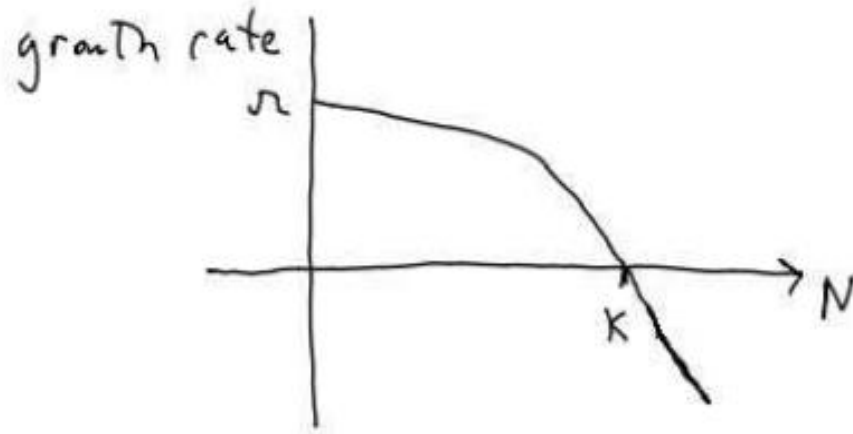
Logistic growth

Eventually, however, resources become depleted and/or the population becomes overcrowded.

Thus as N increases, we expect that r will decrease.

Moreover it can even become negative, meaning that the death rate exceeds the birth rate.

Graphically, we expect that $r(N)$ behaves like

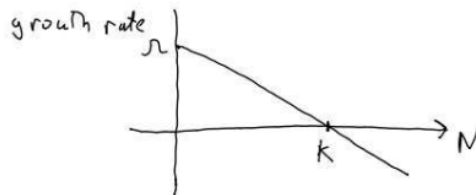


The point at which $r(N) = 0$ is a special population size which neither grows nor decays. It corresponds to $N = K$, where

$K =$ carrying capacity.

In most cases we can't really know the shape of $r(N)$, but the notion of a carrying capacity is itself reasonably sharp.

So the simplest assumption would be to assume that $r(N)$ decreases linearly:



Then

$$r(N) = r \left(1 - \frac{N}{K} \right)$$

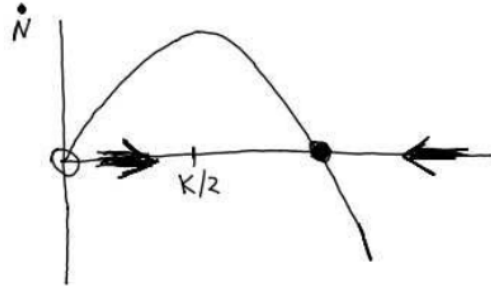
and our growth model now reads

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right), \quad (56)$$

known as the *logistic equation* or the *Verhulst model*.

The logistic equation can be solved exactly but our goals are better served by analyzing it qualitatively.

First, we plot dN/dt vs. N , i.e., we plot the RHS of the logistic equation:



We consider only $N \geq 0$ since populations cannot be negative.

Note that

$$\begin{aligned} \dot{N} &= 0, & N &= 0 \text{ or } K \\ \dot{N} &> 0, & 0 < N < K \\ \dot{N} &< 0, & N > K \end{aligned}$$

We call $N = 0$ and $N = K$ *fixed points* because they correspond to neither growth nor decay. We denote them with asterisks:

$$N_1^* = 0, \quad N_2^* = K.$$

Between $N_1^* = 0$ and $N_2^* = K$, N grows toward K ; conversely, for $N > K$, N decays toward K .

Thus we say that

$$N_1^* = 0 \text{ is } \textit{unstable}$$

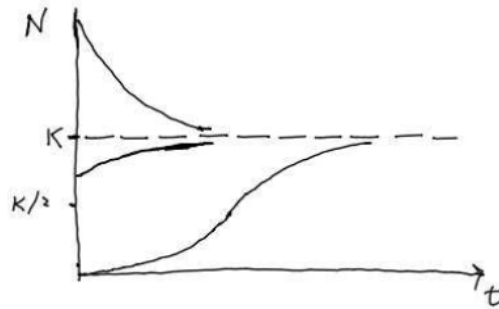
and that

$$N_2^* = K \text{ is } \textit{stable}.$$

Indeed, we see that as long as we initiate growth with $N(0) > 0$, the population always evolves to the carrying capacity.

How it evolves depends on the initial condition:

- Small populations $N < K$ grow exponentially and later slowly towards K , sometimes called *S-shaped* or *sigmoid-shaped* growth.
- Large populations $N > K$ decay exponentially to K .



Although specific details of the logistic model should not be considered as truly representative of population growth, the basic picture of exponential growth followed by saturation is widely but not universally observed.

Hyperbolic growth

One potential criticism of the logistic model concerns the notion of a fixed carrying capacity.

For example, it is possible that, over long time scales, an organism can better dominate its niche as its population increases.

It has also been proposed that species can create niches within which they, or new species that evolved from them, can thrive [52].

An outstanding example of a species with varying K is us: as our population has grown, technology has improved, allowing the population to grow even further.

Thus we consider that

$$K = K(N).$$

We then define the rescaled rate constant

$$r' = r/K(0)$$

so that the logistic equation now reads

$$\frac{dN}{dt} = r'N(K - N).$$

For $K = K(0) = \text{const}$, this is merely a re-expression of equation (56).

Now, however, we imagine that K increases with N like

$$K \sim N^\alpha, \quad N \gg K(0).$$

When $\alpha > 1$, eventually $K \gg N$, and the growth equation is approximated by

$$\frac{dN}{dt} \sim N^{1+\alpha}, \quad \alpha > 1.$$

Separating variables, we have

$$\frac{dN}{N^{1+\alpha}} = dt,$$

which upon integration yields

$$\frac{-1}{1+\alpha} N^{-\alpha} = t + \text{const.}$$

or

$$N^{-\alpha} = (1+\alpha)(t_c - t),$$

where t_c is a re-expression of the original integration constant.

The solution is

$$N(t) \propto (t_c - t)^{-1/\alpha}, \quad t \rightarrow t_c,$$

which exhibits a singular blow-up as $t \rightarrow t_c$, with t_c determined by the initial conditions.

Singular growth is sometimes called *hyperbolic*.

Another mechanism for hyperbolic growth would be to consider the per capita growth rate r to grow with N , like

$$r \sim N^\beta, \quad \beta > 0.$$

Such an expression assumes that growth is not limited by carrying capacity but instead reflects the ability of a population to find more efficient ways to reproduce (or ways to minimize its death rate).

We then have

$$\frac{dN}{dt} = rN \sim N^{1+\beta},$$

and therefore, as above,

$$N(t) \propto (t_c - t)^{-1/\beta}$$

corresponding to hyperbolic growth for $\beta > 0$ (whereas above we required $\alpha > 1$).

In 1960, von Foerster et al. [49] showed that world population for roughly the last millenium fit such a curve, with $\beta \simeq 1$.

Since the fit provided an estimate of t_c , von Foerster's paper, published in Science, was titled *Doomsday: Friday 13 November, A.D. 2026*.

The essential observation here is that human population growth has been super-exponential. Around 1970, however, the growth rate slowed.

Linear stability analysis

We now return to the questions of stability we addressed in Section 8.1.2.

Single species

We write our population model more generally as

$$\dot{N} = F[N(t)].$$

and interpret N as the number of individuals of a particular species.

Fixed points N^* are given by

$$0 = F(N^*).$$

To determine the behavior of the system near a fixed point, we consider small disturbances $x(t)$ so that perturbed populations

$$x(t) = N(t) - N^*.$$

Differentiation both sides yields

$$\dot{x} = \dot{N}.$$

We therefore write

$$\dot{x} = F(N) = F(N^* + x)$$

and we expand F around N^* :

$$F(N^* + x) = F(N^*) + xF'(N^*) + \mathcal{O}(x^2).$$

Noting that the LHS is simply \dot{x} and that $F(N^*) = 0$, we have, neglecting terms of order x^2 and higher,

$$\dot{x} = xF'(N^*). \quad (57)$$

Thus x grows if $F'(N^*) > 0$, and x decays if $F'(N^*) < 0$.

The prediction of this *linear stability analysis* is either exponential growth away from a fixed point or exponential growth towards it.

More specifically, we set

$$a = F'(N^*)$$

and solve the linearization (57) to find that x evolves as

$$x(t) = x(0)e^{at}.$$

Thus

$$\begin{aligned} a < 0 &\Rightarrow N^* \text{ is } \textit{stable} \\ a > 0 &\Rightarrow N^* \text{ is } \textit{unstable} \end{aligned}$$

Of course, the range of stability was already evident from our graphical analysis.

However we now also know the rate $|a|$ at which the system grows away from, or decays toward, the fixed point.

To apply this method to the logistic model (56), we note that

$$a = F'(N^*) = r \left(1 - \frac{2N^*}{K} \right)$$

Then

$$a(N^* = 0) = r$$

and

$$a(N^* = K) = -r.$$

The region of stability therefore depends on the sign of r .

Multiple species

The stability of a multispecies model follows similarly.

We imagine m species, each with an abundance N_i , $i = 1, \dots, m$, that evolves as

$$\dot{N}_i = F_i(N_1, N_2, \dots, N_m), \quad i = 1, \dots, m.$$

The function F_i determines the growth rate of N_i as a function of its interactions with other populations (and itself). The fixed points N_i^* are determined by setting the time derivative to zero:

$$0 = F_i(N_1^*, N_2^*, \dots, N_m^*), \quad i = 1, \dots, m.$$

We expand around the fixed points:

$$N_i(t) = N_i^* + x_i(t), \quad i = 1, \dots, m.$$

where $x_i(t)$ is a perturbation to the i th population.

Neglecting terms of second order and higher in the perturbations, we obtain

$$\frac{dx_i}{dt} = \sum_{j=1}^m x_j \left. \frac{\partial F_i}{\partial N_j} \right|_{\vec{N}=\vec{N}^*}, \quad i = 1, \dots, m.$$

To simplify, we define the *Jacobian matrix* A with elements

$$a_{ij} = \left. \frac{\partial F_i}{\partial N_j} \right|_{\vec{N}=\vec{N}^*}, \quad i, j = 1, \dots, m.$$

In population ecology A is called the *community matrix*. We use it to rewrite the linearized dynamics compactly as

$$\frac{d\vec{x}}{dt} = A\vec{x} \tag{58}$$

where \vec{x} is an $m \times 1$ column vector of the x_i 's.

We seek solutions of the form

$$\vec{x}(t) = e^{\lambda t} \vec{v},$$

where $\vec{v} \neq 0$ and λ is a growth rate.

Inserting into (58), we obtain

$$\lambda e^{\lambda t} \vec{v} = A e^{\lambda t} \vec{v}$$

or

$$A\vec{v} = \lambda\vec{v}. \quad (59)$$

Therefore \vec{v} is an eigenvector of A and λ is an eigenvalue

The eigenvalues and eigenvectors solve the *characteristic equation*

$$\det(A - \lambda I) = 0,$$

where I is the $m \times m$ identity matrix.

Non-trivial solutions occur when the determinant of $A - \lambda I$ vanishes.

In other words, we find the eigenvectors λ by solving

$$\det(A - \lambda I) = 0,$$

and for each eigenvalue we then find the eigenvectors \vec{v} by solving (59).

The general solution of (58) (assuming that all eigenvalues are distinct, and therefore that the eigenvectors are linearly independent) is then the linear combination

$$\vec{x}(t) = c_1 e^{\lambda_1 t} \vec{v}_1 + c_2 e^{\lambda_2 t} \vec{v}_2 + \dots + c_m e^{\lambda_m t} \vec{v}_m$$

where the c_i 's depend on the initial conditions.

In general, the m eigenvalues are complex numbers

$$\lambda = \mu + i\nu$$

that are solutions to an m th order polynomial.

Stability is determined by the sign of largest μ :

$$\begin{aligned}\mu_{\max} < 0 &\Rightarrow \text{stable} \\ \mu_{\max} = 0 &\Rightarrow \text{marginally stable} \\ \mu_{\max} > 0 &\Rightarrow \text{unstable.}\end{aligned}$$

A non-zero imaginary part ν corresponds to oscillations $e^{i\nu t}$ with frequency $2\pi/\nu$.

Predator-prey cycles: the Lotka-Volterra equations

We now illustrate these principles with a simple two-component model of a predator and its prey:

$$\begin{aligned}\dot{N}_1 &= N_1(a - \alpha N_2) \\ \dot{N}_2 &= N_2(-b + \beta N_1).\end{aligned}$$

In this system, known as the *Lotka-Volterra equations*,

$$\begin{aligned}N_1 &= \text{number of prey} \\ N_2 &= \text{number of predators} \\ a &= \text{prey growth rate} \\ b &= \text{predator death rate} \\ \alpha, \beta &= \text{rates of interaction between predators and prey}\end{aligned}$$

a, b, α , and β are all positive.

The fixed points occur where the derivatives vanish. We find one fixed point at

$$\begin{aligned}N_1^* &= b/\beta \\ N_2^* &= a/\alpha\end{aligned}$$

In the notation of the previous section, we have

$$\begin{aligned}F_1(N_1, N_2) &= N_1(a - \alpha N_2) \\ F_2(N_1, N_2) &= N_2(-b + \beta N_1).\end{aligned}$$

The partial derivatives are

$$\begin{aligned}\partial F_1/\partial N_1 &= a - \alpha N_2 \\ \partial F_1/\partial N_2 &= -\alpha N_1 \\ \partial F_2/\partial N_1 &= \beta N_2 \\ \partial F_2/\partial N_2 &= -b + \beta N_1.\end{aligned}$$

and the Jacobian matrix is then

$$A = \left. \frac{\partial F_i}{\partial N_j} \right|_{N_1^*, N_2^*} = \begin{pmatrix} 0 & -\alpha b/\beta \\ \beta a/\alpha & 0 \end{pmatrix}$$

The eigenvalues λ solve

$$\det \begin{vmatrix} -\lambda & -\alpha b/\beta \\ \beta a/\alpha & -\lambda \end{vmatrix} = 0$$

which yields

$$\lambda^2 + ab = 0$$

and therefore

$$\lambda = \pm i\omega, \quad \omega = \sqrt{ab}.$$

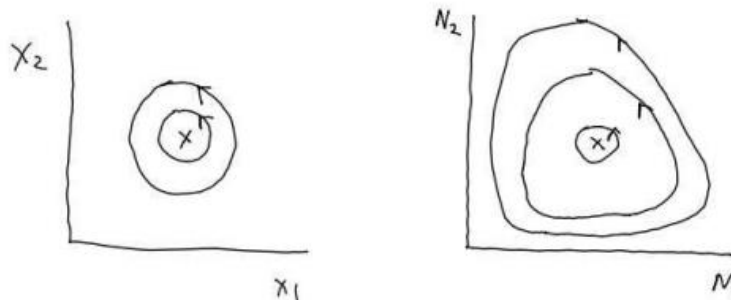
Since $\text{Re}(\lambda) = 0$, the fixed point is marginally stable.

But the non-zero imaginary part means that perturbations to the fixed point are oscillatory, so that

$$\vec{x}(t) = \vec{c}_1 \cos \omega t + \vec{c}_2 \sin \omega t$$

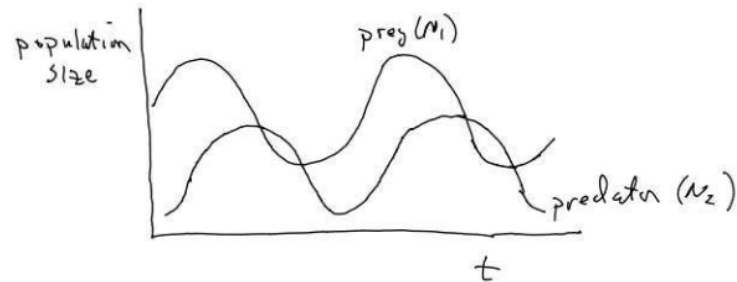
where c_1 and c_2 are related to the initial conditions.

In the *phase space* of x_1 and x_2 , linear stability analysis thus predicts that the perturbed trajectories are simply circles about the fixed point, the radius of which depends on the initial conditions.



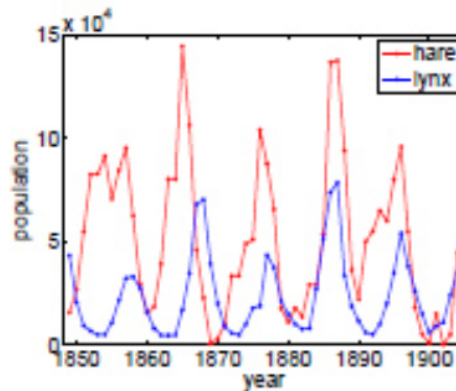
Of course, larger amplitude trajectories depart from the circular shape due to nonlinear effects.

The time functions $x_1(t)$ are simple oscillations. Note, however, that the predator population N_2 is delayed by a quarter-cycle ($\pi/2$) with respect to the prey population N_1 .



Specifically, we see that the growth rate of the predator is fastest when the prey population peaks, and conversely the predator death rate is fastest when the prey population bottoms out.

Remarkably, just such a pattern is found in natural systems. The classic case is that of the 19th century Canadian lynx (predator) and snowshoe hare (prey) populations near Hudson Bay:

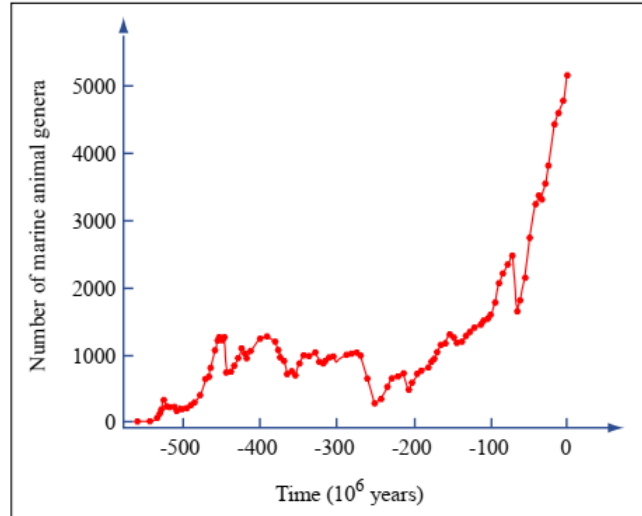


Stability vs. complexity

These considerations raise a big question: *What makes an ecosystem stable?*

We really don't know, but empirically there is abundant evidence that the global ecosystem has changed greatly over long time scales.

As an example, note the Phanerozoic fossil record of biodiversity:



The causes of the fluctuations in this record are likely manifold, and are widely debated.

One issue concerns the relative importance of intrinsic mechanisms of instability compared to extrinsic drivers such as impacts.

We proceed to address the possibility of intrinsic instability within the context of the Lotka-Volterra model.

One question that may be precisely answered is the following: *How is stability related to diversity (i.e., complexity)?*

To address this question, we return to the general formulation of Section 8.2.2, wherein each species potentially interacts with $m - 1$ others:

$$\dot{N}_i = F_i(N_1, N_2, \dots, N_m), \quad i = 1, \dots, m.$$

From linear stability analysis, we found that perturbations from fixed points evolve like

$$\frac{d\vec{x}}{dt} = A\vec{x},$$

and that a fixed point is stable if, among the eigenvalues $\lambda = \mu + i\nu$ of A , we have $\mu_{\max} < 0$.

We now focus entirely on the community matrix A .

We require that each species be by itself stable, so that if perturbed individually from its fixed point it relaxes back to it.

We take each time constant to be unity, so that

$$a_{ii} = -1.$$

Next, we allow interactions between species i and j via a matrix made of off-diagonal terms b_{ij} .

As in the construction of a random graph or food web, we allow only only a fraction $0 < C < 1$ of all possible interactions, so that

$$b_{ij} = 0 \quad \text{with probability } 1 - C.$$

The values of the non-zero b_{ij} give the strength and sign of the interaction between species i and j . We choose them randomly, with zero mean and variance s^2 :

$$\text{with probability } C : \quad \langle b_{ij} \rangle = 0 \text{ and } \langle b_{ij}^2 \rangle = s^2.$$

Assembling both pieces, the $m \times m$ community matrix

$$A = B - I.$$

A is stable only if each of its eigenvalues have negative real parts.

Thus one would like to know, as a function of the the system size m , the connectance C , and the standard deviation s , the probability

$$P(m, C, s) = \text{probability of stability}$$

The *May-Wigner stability theorem* states [47, 54]

$$\begin{aligned} P &\rightarrow 1 \quad \text{if } s(mC)^{1/2} < 1 \\ P &\rightarrow 0 \quad \text{if } s(mC)^{1/2} > 1. \end{aligned}$$

Thus we have an answer to our question about the relation of stability to complexity.

Complexity can be interpreted in two ways: as the size m (i.e., diversity) of the ecosystem, or as its connectivity C .

As either increases, the “equilibrium ecosystem” loses its stability.

This conclusion is easily understood qualitatively. Since the eigenvalues λ_B of B satisfy

$$B\vec{x} = \lambda_B\vec{x}$$

and, by definition,

$$I\vec{x} = \vec{x},$$

then, since $A = B - I$,

$$A\vec{x} = (\lambda_B - 1)\vec{x},$$

i.e., the eigenvalues of A are given by

$$\lambda = \lambda_B - 1.$$

The essential statement, therefore, is that as B becomes large in dimension, as the fraction of its non-zero elements increases, and/or as the magnitude of its elements increase, eventually the real part of one of its eigenvalues exceeds unity, so that A becomes is unstable.

Discrete logistic model

Return now to the logistic model (56) for a single population:

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right).$$

Now imagine that we care only about the population changes from, say, year to year, and we take N_j to be the population in the j th year.

Then the differential equation becomes the difference equation

$$N_{j+1} - N_j = rN_j \left(1 - \frac{N_j}{K} \right)$$

or

$$N_{j+1} = (1 + r)N_j - \frac{r}{K}N_j^2.$$

Now rescale the populations to the new variable

$$x_{j+1} = \frac{r/K}{1+r}N_j,$$

which yields

$$(1 + r)x_j = (1 + r)^2x_j - (1 + r)^2x_j^2.$$

Setting

$$4\mu = 1 + r$$

we then obtain the *discrete logistic equation*

$$x_{j+1} = 4\mu x_j(1 - x_j).$$