ICTS Lecture notes Allesina

Stefano Allesina

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# 1 The Generalized Lotka-Volterra model

1.1 History

Alfred J. Lotka (1880-1949) was born to French-speaking American parents in Lemberg (then part of the Habsburg empire, now Lviv, Ukraine). He studied in France, Germany and England, receiving a BSc in 1901 and a DSc in 1912 from Birmingham university. He moved to the US in 1902, and worked at the US Patent office, as an editor of Scientific American, and as a statistician at the Metropolitan Life Insturance Company in NYC. He wrote more than a hundred papers and five books, spanning a wide range of topics. He's best known for the book *Elements of Physical Biology*, his contributions to demography, and one of the first studies dealing with bibliometrics.

Starting in 1910, he investigated coupled differential equations relating to chemical as well as ecological dynamics. In 1920 he studied a system of two ODEs that gave rise to perpetual oscillations: *"It was, therefore, with considerable surprise that the writer, on applying his method to certain special cases, found these to lead to undamped, and hence indefinitely continued, oscillations."* He went on to describe *"1. A species of organism S_1, a plant species, say, deriving its nourishment from a source presented in such large excess that the mass of the source may be considered constant during the period of time with which we are concerned. 2. A species S_2, for example a herbivorous animal species, feeding on S_1."*

The equations he had derived (and then studied in more detail) are now called Lotka-Volterra equations.

Vito Volterra (1860-1940) was born in Ancona (then part of the Papal State) in a poor Jewish family. The financial situation precipitated with the death of his father, when Vito was two. Vito and his mother went to live with relatives in Turin and then Florence. Volterra showed amazing mathematical talent at a very young age. Antonio Roiti, professor of physics in Florence, noticed the budding mathematician and hired him as his assistant, so that he could continue his studies. He went on to enroll at the Scuola Normale in Pisa, receiving a degree in Physics in 1882. At age

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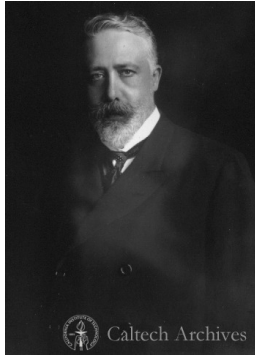
23 he was made full professor of Rational Mechanics in Pisa, and then in 1900 of Mathematical Physics in Rome. For thirty years, he contributed important studies in mathematics, and enriched academic life in Italy (for example, he was the first director of the National Center for Research). In 1931 he refused to take an oath of loyalty to the fascist regime (only 12 professors out of 1250 refused), and was therefore forced to resign (his take on the fascist enterprise: *"Empires die, but Euclid's theorems keep their youth forever"*).

His interest in mathematical ecology is due to Umberto D'Ancona (his son-in-law), who had studied the trends in fisheries in the Adriatic sea before and immediately after WWI. In 1914-1918 fisheries in the Adriatic had stopped completely because of the conflict. D'Ancona had noticed that, while herbivorous fish had remained about constant, the piscivorous fish had increased dramatically in number. The problem piqued Volterra, who immediately published a sophisticated study, proposing the same equations studied by Lotka. In a short letter to Nature 1926, he stated the so-called "Volterra's Effect" (which he termed "Law III"): *"a complete closure of the fishery was a form of 'protection' under which the voracious fishes were much the better and prospered accordingly, but the ordinary food-fishes, on which these are accustomed to prey, were worse off than before."* This brief paper was a summary of a much more extensive study published in Italian.

Lotka-Volterra interactions

In 1927, Lotka wrote to Nature to raise the issue that the equations studied by Volterra and the figures presented in Volterra's brief article were identical to those found in *Elements of Physical Biology* (published in 1925). He concluded: *"It would be gratifying if Prof. Volterra's publication should direct attention to a field and method of inquiry which apparently has hitherto passed almost unnoticed."*

Volterra graciously conceded *"I recognize his priority, and am sorry not to have known his work, and therefore not have been able to mention it."* He however listed a few points in which the two authors had pursued different directions, and concluded *"Working independently the one from the other, we have found some common results, and this confirms the exactitude and the interest in the position of the problem. I agree with him in his conclusions that these studies and these methods of research deserve to receive greated attention from scholars, and should give rise to important applications."*
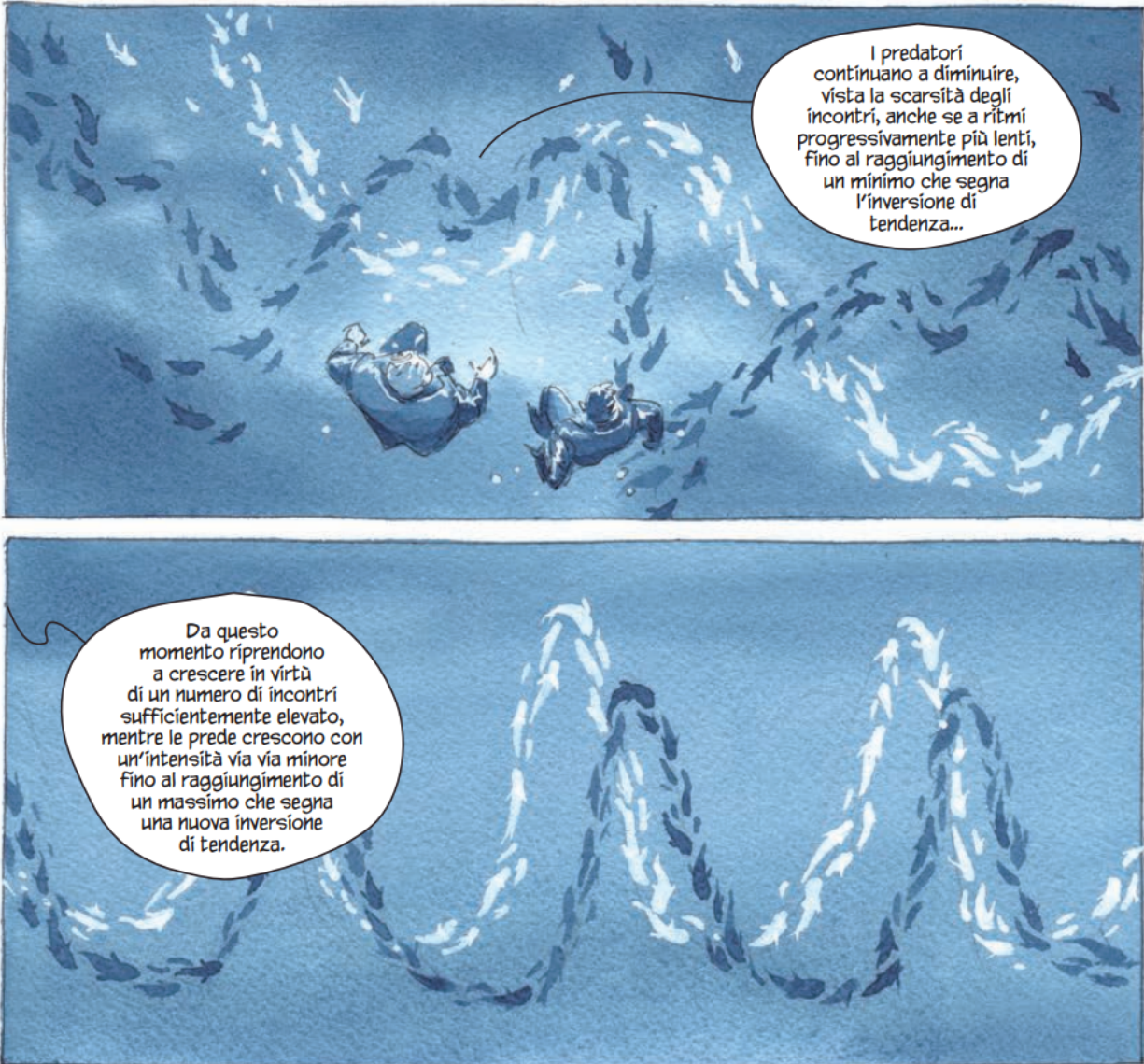
Vito Volterra and Umberto D'Ancona explore the Lotka-Volterra model. Taken from the fantastic La funzione del mondo, *a graphic novel on Volterra by Bilotta and Grillotti.*

1.2 Equations

We can write the GLV model for n interacting populations in component form as:

$$\frac{dx_i(t)}{dt} = \dot{x}_i = x_i \left(r_i + \sum_j A_{ij} x_j \right)$$

and in matrix form as:

$$\dot{x} = D(x)\left(r + Ax\right)$$

4

where $x = x(t)$ is a (column) vector of length n containing the densities of all populations $1, \ldots, n$ at time t, r is a vector of *intrinsic growth rates* (or death rates, when negative), measuring the growth (decline) of population i when growing alone at low density, and A is a $n \times n$ matrix of *interaction coefficients*. We use $D(x)$ to denote the diagonal matrix with x on the diagonal.

Sometimes the model is written in a slightly different way, by bringing the vector r outside the parenthesis:

$$
\begin{aligned}
\dot{x}_i &= x_i \left(r_i + \sum_j A_{ij} x_j \right) \\
&= r_i x_i \left(1 + \frac{1}{r_i} \sum_j A_{ij} x_j \right) \\
&= r_i x_i \left(1 + \sum_j B_{ij} x_j \right)
\end{aligned}
$$

where we have defined $B_{ij} = A_{ij}/r_i$. In matrix form, we obtain:

$$
\dot{x} = D(x \circ r) \left(1_n + Bx \right)
$$

where $\circ$ is the Hadamard (element by element) product. This notation is convenient when computing the equilibria of the system; the previous notation is more convenient when investigating their stability. We will alternate between the two notations, using A and $B = D(r)^{-1}A$ for the two matrices.

1.3 Equilibria

If an equilibrium $x^\star$ in which all populations are present exists, it must be the solution of

$$
\begin{aligned}
1_n + Bx^\star &= 0_n \\
Bx^\star &= -1_n \\
x^\star &= -B^{-1}1_n
\end{aligned}
$$

when the matrix B is invertible. Naturally, the equilibrium must be positive (called *feasible*) to be biologically attainable.

For example, consider:

$$
A = \begin{pmatrix} -4 & -1 & -3 \\ -14 & -8 & -10 \\ -6 & -15 & -13 \end{pmatrix} \quad r = \begin{pmatrix} 8 \\ 32 \\ 34 \end{pmatrix} \quad B = D(r)^{-1}A = \begin{pmatrix} -\frac{1}{2} & -\frac{1}{8} & -\frac{3}{8} \\ -\frac{7}{16} & -\frac{1}{4} & -\frac{5}{16} \\ -\frac{3}{17} & -\frac{15}{34} & -\frac{13}{34} \end{pmatrix}
$$

There is an equilibrium when at which all populations are present:

$$x^\star = -A^{-1}r = -B^{-1}1_n = \begin{pmatrix} 1 \\ 1 \\ 1 \end{pmatrix}$$

If the matrix B is rank-deficient (and thus singular) there are infinitely many equilibria; for example, if the rank of B is $n-1$ there are infinitely many equilibria belonging to a line in $\mathbb{R}^n$.

When B is nonsingular, the model admits at most one positive equilibrium in which all populations are present. However, there can be up to $2^n - 1$ equilibria in which *one or more populations are absent/extinct*. Call $B^{(k,k)}$ the submatrix of B obtained by retaining the rows and columns indexed by the set k. Then by solving

$$B^{(k,k)}x^{(k)\star} = -1_{\|k\|}$$

we obtain an equilibrium for the subcommunity where only the populations in k are present (provided that the equilibrium is feasibile).

For the example above, we have:

$$B^{(\{1,2\},\{1,2\})} = \begin{pmatrix} -\frac{1}{2} & -\frac{1}{8} \\ -\frac{7}{16} & -\frac{1}{4} \end{pmatrix}$$

and

$$x^{(\{1,2\})\star} = -(B^{(\{1,2\},\{1,2\})})^{-1}1_2 = \begin{pmatrix} \frac{16}{9} \\ \frac{8}{9} \end{pmatrix}$$

Therefore, the subsystem in which only the first two populations are present yields a feasible equilibrium.

Similarly,

$$x^{(\{1,3\})\star} = \begin{pmatrix} \frac{1}{17} \\ \frac{44}{17} \end{pmatrix} \quad x^{(\{1\})\star} = \begin{pmatrix} 2 \end{pmatrix} \quad x^{(\{2\})\star} = \begin{pmatrix} 4 \end{pmatrix} \quad x^{(\{3\})\star} = \begin{pmatrix} \frac{34}{13} \end{pmatrix}$$

The subsystem in which only populations 2 and 3 are present does not yield a feasible equilibrium.

1.4 Types of dynamics

For a single population, the GLV model can yield only two outcomes: unbounded growth, or convergence to an equilibrium; if the equilibrium is $x^\star = 0$, we say that the population is extinct at the equilibrium.

When we have two populations, we can also observe neutral cycles (as in the classic LV predator-prey system), and bistability (i.e., one population survives, while the other goes extinct; the identity of the population going extinct depends on the initial conditions).

For three populations we can observe limit cycles.

For four or more populations we can have chaos (i.e., non-periodic oscillations).

1.5 Equilibrium as time-average

Suppose that $x(t)$ has a periodic orbit, of period T (i.e., we assume $x(0) = x(T)$). Further, assume that the GLV has a feasible, interior equilibrium $x^\star$. We want to calculate the average density for each population:

$$\frac{1}{T} \int_0^T x(t) dt$$

First, we assume that $x(t) > 0$ and write the dynamics of its logarithm:

$$\frac{d \log(x_i(t))}{dt} = \frac{1}{x_i(t)} \frac{dx_i(t)}{dt} = r_i + \sum_j A_{ij} x_j(t)$$

In vector form:

$$\frac{d \log x(t)}{dt} = r + Ax(t)$$

Compute the average on both sides:

$$\frac{1}{T} \int_0^T \frac{d \log(x(t))}{dt} dt = \frac{1}{T} \int_0^T (r + Ax(t)) \, dt$$

yielding:

$$\frac{1}{T} (\log(x(T)) - \log(x(0))) = 0_n = r + A \left(\frac{1}{T} \int_0^T x(t) dt \right)$$

Note that the l.h.s. is zero because $x(0) = x(T)$. Now rearrange:

$$-r = A \left(\frac{1}{T} \int_0^T x(t) dt \right)$$

Multiplying by the matrix inverse:

$$-A^{-1} r = x^\star = \frac{1}{T} \int_0^T x(t) dt$$

showing that *the average density is* in fact *the equilibrium*. With a similar argument, one can prove that if the trajectory stays in a compact space (i.e., in case of chaotic attractors), then the long-time average is still $x^\star$.

A dynamical system is permanent if, for all $x_i(0) > 0$, the limit $\liminf_{t \to \infty} x_i(t) > \delta > 0$ for all i. This means that each axis of $\mathbb{R}^n$ *repels* the dynamics when t is large enough.

Suppose that a GLV system is permanent, and that population dynamics converge to a limit cycle or a chaotic attractor; then, because of the calculation above, there must be a positive equilibrium in $\mathbb{R}^n$. Thus, a GLV system without a feasible equilibrium cannot be permanent. That is to say, the coexistence of all populations in a GLV system *requires* a feasible equilibrium.

1.6 Local stability

We want to determine whether an equilibrium point is locally asymptotically stable; this means that, for sufficiently small perturbations of the equilibrium, $x(0) = x^\star + \epsilon$, we have that $\lim_{t \to \infty} x(t) = x^\star$. Let's start by considering the case of a single population:

- Take an ODE $dx/dt = f(x)$
- The population is resting at an equilibrium $x^\star$
- We perturb the population abundance, and track the dynamics when starting at $x(0) = x^\star + \epsilon$, where ϵ (the perturbation) is taken to be sufficiently small $\|\epsilon\| \ll 1$
- We write $\Delta x(0) = x(0) - x^\star$
- We derive the dynamics for Δx.

By chain rule,

$$
\begin{aligned}
\frac{d\Delta x}{dt} &= \frac{d\Delta x}{dx}\frac{dx}{dt} \\
&= 1\frac{dx}{dt} \\
&= f(x) \\
&= f(\Delta x + x^\star)
\end{aligned}
$$

Where we have substituted $x = \Delta x + x^\star$.

- Now we approximate the function $f(\Delta x + x^\star)$ by Taylor-expanding.

> **i** Taylor series
>
> We can approximate the behavior of a (infinitely differentiable) function in the vicinity of a point a by a power series:
>
> $$f(x) = f(a) + \frac{1}{1!}\left.\frac{df(x)}{dx}\right|_a (x-a) + \frac{1}{2!}\left.\frac{d^2f(x)}{dx^2}\right|_a (x-a)^2 + \frac{1}{3!}\left.\frac{d^3f(x)}{dx^3}\right|_a (x-a)^3 + \ldots$$
>
> where $n! = n(n-1)(n-2)\ldots 1$ is the factorial function and the derivatives are evaluated at a. When we choose $a = 0$, this is called the Maclaurin series.
> **Example**
> Expand e^x around 0:

$$e^x = e^0 + e^x|_0 \, x + \frac{1}{2} \, e^x|_0 \, x^2 + \frac{1}{6} \, e^x|_0 \, x^3 + \dots$$

$$= 1 + x + \frac{1}{2}x^2 + \frac{1}{6}x^3 + \dots$$

$$= \sum_{k=0}^{\infty} \frac{x^k}{k!}$$

We want to Taylor-expand $f(x) = f(\Delta x + x^\star)$ around $x^\star$:

$$f(x) = f(x^\star) + \left.\frac{df(x)}{dx}\right|_{x^\star} (x - x^\star) + \frac{1}{2} \left.\frac{d^2 f(x)}{dx^2}\right|_{x^\star} (x - x^\star)^2 + \dots$$

Note that $f(x^\star) = 0$ by the definition of an equilibrium. If the deviation is small, we can neglect all the higher-order terms, obtaining:

$$\frac{d\Delta x}{dt} = f(x) \approx \left.\frac{df(x)}{dx}\right|_{x^\star} \Delta x$$

which is the equation of the exponential growth model, with $\rho = \left.\dfrac{df(x)}{dx}\right|_{x^\star}$. Then, the solution is $\Delta x(t) = \Delta x(0)e^{\rho t}$, and the deviation from the equilibrium eventually reaches zero (i.e., the system goes back to $x^\star$) whenever $\rho < 0$.

For example, take the logistic growth model $\dot{x} = x(1 - x)$, and evaluate the stability of $x^\star = 1$; we have:

$$\left.\frac{df(x)}{dx}\right|_{x^\star} = \left.\frac{d(x - x^2)}{dx}\right|_{x^\star} = (1 - 2x)|_{x^\star} = -1$$

and thus the equilibrium is *locally asymptotically stable*. Locally, because we have considered very small deviations from the equilibrium, and asymptotic because convergence only happens eventually.

In analogy with the Taylor-expansion of functions of a single variable, we can write:

$$f_i(x^\star + \Delta x) = f_i(x^\star) + \sum_k \left.\frac{\partial f_i(x)}{\partial x_k}\right|_{x^\star} \Delta x_k + \frac{1}{2} \sum_k \sum_l \left.\frac{\partial^2 f_i(x)}{\partial x_k \partial x_l}\right|_{x^\star} \Delta x_k \Delta x_l + \cdots$$

As before, $f_i(x^\star) = 0$, and if we take only the second term (i.e., the term linear in Δx) we can approximate the function as:

$$f_i(x^\star + \Delta x) \approx \sum_k J_{ik}|_{x^\star} \, \Delta x_k$$

Where we have defined the *Jacobian* matrix J:

$$J_{ij} = \frac{\partial f_i(x)}{\partial x_j}$$

For each equilibrium of the system, we can obtain a different *community matrix* (the name is due to Richard Levins) M:

$$M = J\big|_{x^\star}$$

As such, a system of ODEs has a *single* Jacobian, and as many community matrices as there are equilibria. As before, we assume that we have slightly perturbed the system at equilibrium, $x(t) = x^\star + \Delta x$, where Δx is assumed to be small, and then we approximate the dynamics:

$$\frac{d\Delta x}{dt} \approx J\big|_{x^\star} \Delta x$$

i.e., we need to solve a linear system of ODEs.

> ### ℹ Solving systems of linear ODEs
>
> Consider the system of first-order, autonomous ODEs:
>
> $$\frac{dx}{dt} = Ax$$
>
> If the matrix A is diagonalizable, we can decompose the matrix as:
>
> $$A = Q\Lambda Q^{-1}$$
>
> We define a new system of equations, by changing the variables:
>
> $$y = Q^{-1}x \quad x = Qy$$
>
> Then, by chain rule:
>
> $$\frac{dy}{dt} = Q^{-1}\frac{dx}{dt} = Q^{-1}Q\Lambda Q^{-1}x = \Lambda Q^{-1}x = \Lambda y$$
>
> We have decoupled all equations: now the y_i grow or decline independently of each other.
>
> $$\frac{dy_i}{dt} = \lambda_i y_i$$
>
> This is in fact the equation for the exponential growth/decay, with solution $y_i(t) = y(0)e^{\lambda_i t}$. We can bring these solutions back to the original form:
>
> $$y(t) = e^{\Lambda t}y(0)$$
>
> where $e^{\Lambda t}$ is a diagonal matrix:
>
> $$e^{\Lambda t} = \begin{pmatrix} e^{\lambda_1 t} & 0 & \cdots & 0 \\ 0 & e^{\lambda_2 t} & \cdots & 0 \\ \cdots & \cdots & \cdots & \cdots \\ 0 & 0 & \cdots & e^{\lambda_n t} \end{pmatrix}$$

Then:

$$x(t) = Qy(t) = Qe^{\Lambda t}y(0) = Qe^{\Lambda t}Q^{-1}x(0)$$

Allowing to easily compute the solution for any linear systems of ODEs.

Stability of the origin

Suppose that λ_i is a real, negative number; then $\lim_{t\to\infty} e^{\lambda_i t} = 0$. If λ_i is positive, on the other hand, then $\lim_{t\to\infty} e^{\lambda_i t} = \infty$. Thus, if any of the $\lambda_i > 0$, the system will initially move toward ∞ in the direction specified by the corresponding eigenvector.

Whenever λ_i is complex (e.g., generically, when A is not symmetric), then we need to consider:

$$e^{\alpha t + i\beta t} = e^{\alpha t}e^{i\beta t} = e^{\alpha t}(\cos\beta + i\sin\beta)t$$

where we have used Euler's formula. Importantly, $(\cos\beta + i\sin\beta)$ is bounded, and in fact its real (imaginary) part is ≤ 1 (the equation describes a unit circle in the complex plane). Then, $\lim_{t\to\infty} e^{\alpha t + i\beta t} = 0$ if $\alpha < 0$.

Therefore, the vector 0_n is an asymptotically stable equilibrium of the system $\dfrac{dx}{dt} = Ax$ if and only if *all* the eigenvalues of A have negative real part.

Stability of the origin for $A_{2\times2}$

As we have shown above, the eigenvalues of a 2×2 matrix A:

$$A = \begin{pmatrix} a & b \\ c & d \end{pmatrix}$$

are:

$$\lambda = \frac{a + d \pm \sqrt{4bc + (a-d)^2}}{2}$$

We can rewrite the values as:

$$\lambda = \frac{1}{2}\left(\mathrm{Tr}A \pm \sqrt{(\mathrm{Tr}A)^2 - 4\det A}\right)$$

If the trace is negative, and the determinant positive, then the eigenvalues have negative real part, and thus the origin is stable for the corresponding system of linear ODEs. In fact, knowing the trace and the determinant is in this case sufficient to determine the type of dynamics around equilibrium:
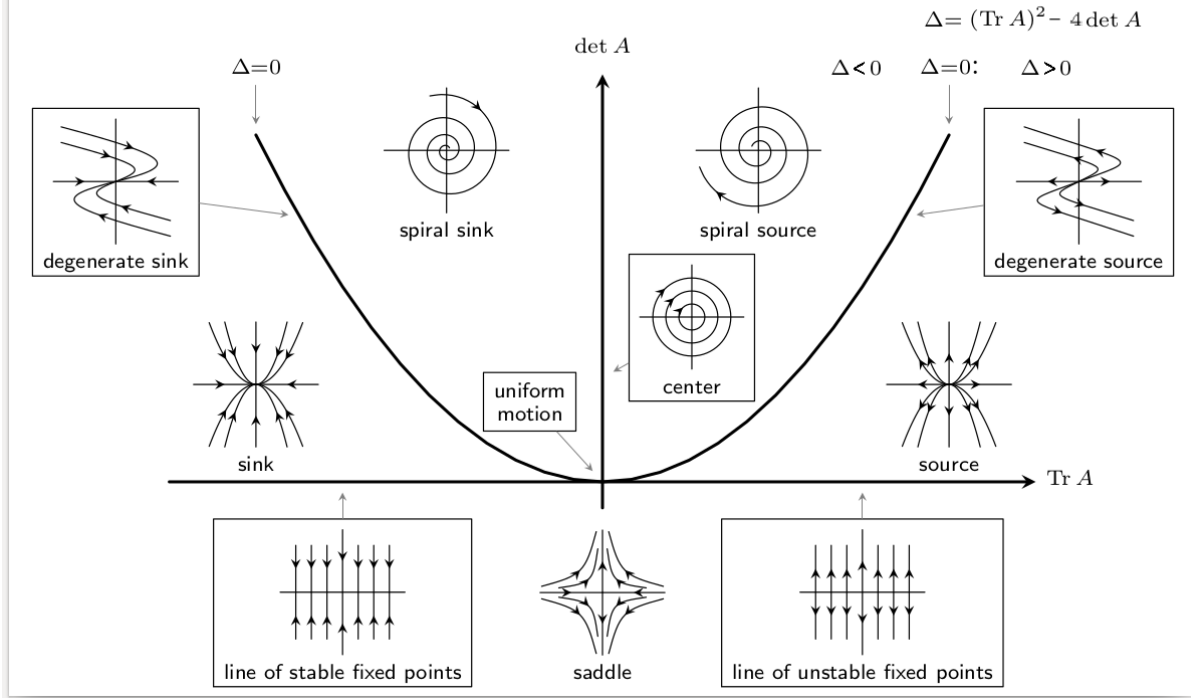
Figure 1: Characterizing dynamics using trace and determinant

To probe the local asymptotic stability of the equilibria, we can:

- Calculate the Jacobian matrix, J
- Plug in an equilibrium, obtaining the corresponding community matrix M
- Compute the eigenvalues of M, λ_i
- If *all* the eigenvalues have negative real part, $\Re(\lambda_i) < 0$, then the equilibrium is locally asymptotically stable; if *any* $\Re(\lambda_i) > 0$, then the equilibrium is unstable, and there are small perturbations that will amplify (at least initially)

For the GLV system with equilibrium $x^\star = -A^{-1}r > 0_n$, we have:

$$J_{ii} = \frac{\partial(r_i x_i + \sum_j A_{ij} x_i x_j)}{\partial x_i} = r_i + \sum_j A_{ij} x_j + A_{ii} x_i$$

At equilibrium, we have:

$$r_i + \sum_j A_{ij} x_j^\star = 0$$

and therefore

$$M_{ii} = J_{ii}\big|_{x^\star} = A_{ii} x_i^\star$$

Similarly,

$$J_{ii} = \frac{\partial(r_i x_i + \sum_j A_{ij} x_i x_j)}{\partial x_j} = A_{ij} x_i$$

and thus

$$M_{ij} = J_{ij}\big|_{x^\star} = A_{ij} x_i^\star$$

Putting them together, we obtain:

$$M = J\big|_{x^\star} = D(x^\star) A$$

and thus the equilibrium is l.a.s. if and only if all of the eigenvalues of $D(x^\star)A$ have negative real part.

If the matrix A is symmetric, any feasible equilibrium is stable if and only if the eigenvalues of A are all negative (i.e., A is negative definite). To prove this, take $A = A^T$ and consider the similarity transformation

$$D(x^\star)^{-\frac{1}{2}} D(x^\star) A D(x^\star)^{\frac{1}{2}}$$
$$D(x^\star)^{\frac{1}{2}} A D(x^\star)^{\frac{1}{2}}$$

The matrices $D(x^\star)A$ and $D(x^\star)^{\frac{1}{2}} A D(x^\star)^{\frac{1}{2}}$ are *similar*, and thus have the same eigenvalues; the matrices A and $D(x^\star)^{\frac{1}{2}} A D(x^\star)^{\frac{1}{2}}$ are *congruent*, and thus have the same number of positive, negative and zero eigenvalues by Sylvester's law of inertia.

A symmetric matrix is negative definite if all its submatrices obtained by deleting a set of rows and the corresponding columns are negative definite as well. Then, if $A = A^T$ is negative definite, a) a feasible equilibrium is locally stable, and b) for any subsystem, feasibility implies local stability.

Note that this is generally not the case for nonsymmetric matrices A, in which case we could have that A has all eigenvalues with a negative real part, while $D(x^\star)A$ has some eigenvalues with positive real part (or viceversa). For example, take

$$A = \begin{pmatrix} -3 & 4 & 0 \\ 5 & -2 & -2 \\ 5 & 5 & -3 \end{pmatrix} \quad \lambda(A) = \{-7, \frac{1}{2}(-1 \pm i\sqrt{15})\}$$

and the equilibrium $x^\star = (1, 1, 1/2)^T$ (obtained for $r = (-1, -2, -17/2)$); we obtain:

$$M = D(x^\star)A = \begin{pmatrix} -3 & 4 & 0 \\ 5 & -2 & -2 \\ \frac{5}{2} & \frac{5}{2} & -\frac{3}{2} \end{pmatrix} \quad \lambda(B) = \{-7, \frac{1}{4}(1 \pm i\sqrt{31})\}$$

Thus, the equilibrium is not locally asymptotically stable.

1.7 Global asymptotic stability

In certain models, we can show that whenever all the populations start at a positive value, they will always reach a certain equilibrium $x^\star$. In this case, we say the equilibrium is globally asymptotically stable.

Because solving differential equations is in general very difficult, and in many cases of interest impossible, we employ a proxy function, called a Lyapunov function.

> **i Lyapunov functions**
>
> We want to prove that all trajectories originating at $x(0) > 0$ eventually converge to $x^\star$. If we can find a function V such that:
>
> - $V(x(t)) \geq 0$ for all $x(t) > 0$
> - $V(x(t)) = 0$ if and only if $x(t) = x^\star$
> - $\dfrac{dV(x(t))}{dt} \leq 0$ for all $x(t)$ and
> - $\dfrac{dV(x(t))}{dt} = 0$ if and only if $x(t) = x^\star$
>
> then $x^\star$ is globally asymptotically stable: all trajectories starting at a positive point will converge to it.
> The logic of this procedure is to identify a suitable function V that is positive everywhere but at the equilibrium, and is always declining in time; then necessarily the function will eventually reach zero, which is attained only at equilibrium.
> **Example**
> $V(x(t)) = (x(t) - x^\star)^2$ is a Lyapunov function for the logistic growth model $dx/dt = x(1 - x)$: the model has an equilibrium $x^\star = 1$ that is globally asymptotically stable.
>
> - $V(x(t))$ is always nonnegative, and is zero only at $x(t) = x^\star = 1$
> - The derivative of $V(x(t))$ w.r.t. time is:
>
> $$\frac{dV(t)}{dt} = \frac{dV(t)}{dx(t)} \frac{dx(t)}{dt}$$
> $$= 2(x(t) - x^\star)\frac{dx(t)}{dt}$$
> $$= -2(x(t) - 1)x(t)(x(t) - 1)$$
> $$= -2x(t)(x(t) - 1)^2 \leq 0$$

There are two classic candidate Lyapunov functions for Lotka-Volterra models. The first is due to MacArthur, and shows that, when interactions are symmetric and the matrix of interactions is negative definite (i.e., has only negative eigenvalues), the feasible equilibrium is globally stable.

We consider a slightly modified version of MacArthur's function, and assume $A = A^T$:

$$W(x) = r^T x^\star - (2r^T x + x^T A x)$$

Whenever A is negative definite, then $W(x(t))$ is positive everywhere but at equilibrium (the function is convex), and has a single minimum at the equilibrium. Note that, whenever $x^\star > 0_n$ is an equilibrium, then

$$r + Ax^\star = 0_n$$
$$r = -Ax^\star$$

Substitute these values in the function W, to obtain:

$$
\begin{aligned}
W(x^\star) &= r^T x^\star - (2r^T x^\star + (x^\star)^T A x^\star) \\
&= r^T x^\star - (2r^T x^\star + ((x^\star)A)^T x^\star) \\
&= r^T x^\star - (2r^T x^\star - r^T x^\star) \\
&= 0_n
\end{aligned}
$$

Differentiating with respect to time, we find:

$$
\begin{aligned}
\dot{W}(x(t)) &= -(2r^T \dot{x} + \dot{x}^T A x + x^T A \dot{x}) \\
&= -(2r^T \dot{x} + \dot{x}^T A^T x + x^T A \dot{x}) \\
&= -2(r + Ax)^T \dot{x} \\
&= -2(r + Ax)^T D(x)(r + Ax) \\
&= -2 \sum_i x_i (r_i + (Ax)_i)^2 \leq 0
\end{aligned}
$$

A more general candidate Lyapunov function is due to Goh, and shows that, whenever there exists a positive diagonal matrix $D(w)$ such that $D(w)A^T + AD(w)$ is negative definite, then the equilibrium $x^\star > 0_n$ is globally stable.

We start with the simplest case in which $w = 1_n$ and thus $D(w) = I$. Take the function

$$V(x(t)) = \sum_i \left(x_i - x_i^\star - x_i^\star \log \frac{x_i}{x_i^\star} \right)$$

The function is positive for every $x \in \mathbb{R}_+^n$, because $z - 1 - \log z \geq 0$ whenever $z > 0$; take $z = x_i/x_i^\star$ and then multiply by $x_i^\star$ to prove that the function is nonnegative.

Differentiating with respect to time, we find:

$$\dot{V}(x(t)) = \sum_i \left(\dot{x}_i - x_i^\star \frac{\dot{x}_i}{x_i} \right)$$

$$= \sum_i (x_i(r_i + (Ax)_i) - x_i^\star(r_i + (Ax)_i))$$

$$= \sum_i \Delta x_i(-(Ax^\star)_i + (Ax)_i)$$

$$= \sum_{i,j} \Delta x_i A_{ij} \Delta x_j$$

$$= \Delta x^T A \Delta x$$

$$= \frac{1}{2} \Delta x^T (A + A^T) \Delta x$$

Thus, if the symmetric part of A, $H(A) = \frac{1}{2}(A + A^T)$ is negative definite, then $\dot{V}(x(t)) < 0$ for every $\Delta x \neq 0$ and the equilibrium is stable.

To extend the reach of the candidate function, consider the change of variables:

$$z_i = x_i/w_i \quad x_i = w_i z_i$$

with $w_i > 0$. This change of variables cannot impact the existence or stability of equilibria (we are simply changing the units of measure we are using to measure the density of each population). Then,

$$\dot{z}_i = \frac{\dot{x}_i}{w_i} = \frac{x_i}{w_i}(r_i + (Ax)_i) = z_i(r_i + (AD(w)z)_i) = z_i(r_i + (\tilde{A}z)_i)$$

Thus, if $H(\tilde{A}) = \frac{1}{2}(AD(w) + D(w)A^T)$ is negative definite, the equilibrium is stable.

1.8 Global stability and saturated equilibria

When Goh's function holds, we can prove that dynamics starting from positive conditions $x(t) > 0_n$ will converge to a *saturated equilibrium* $\tilde{x}$ characterized by two conditions. We have n populations, and at the saturated equilibrium the populations in set k coexist at a globally stable equilibrium, and the remaining populations, belonging to set $n - k$ are extinct, and cannot re-invade the system starting from low abundance.

Without loss of generality, we can order the populations such that the first $\|k\|$ populations are those that coexist at the saturated equilibrium, and the remaining $\|n - k\|$ are those extinct at the saturated equilibrium. We partition all variables according to the two sets:

$$x = \begin{pmatrix} y \\ z \end{pmatrix} \quad \tilde{x} = \begin{pmatrix} y^\star \\ 0_{n-k} \end{pmatrix} \quad A = \begin{pmatrix} \mathfrak{A} & \mathfrak{B} \\ \mathfrak{C} & \mathfrak{D} \end{pmatrix} \quad r = \begin{pmatrix} \mathfrak{r} \\ \mathfrak{s} \end{pmatrix}$$

We consider a minor modification of Goh's function:

$$V(x(t)) = \sum_{i \in k} \left(y_i - y_i^\star - y_i^\star \log \frac{y_i}{y_i^\star} \right) + \sum_{i \in n-k} z_i$$

Differentiating with respect to time, we obtain:

$$\dot{V}(x(t)) = \sum_{i \in k} \left(\dot{y}_i - y_i^\star \frac{\dot{y}_i}{y_i} \right) + \sum_{i \in n-k} \dot{z}_i$$
$$= \Delta y^T (\mathfrak{r} + \mathfrak{A}y + \mathfrak{B}z) + z^T (\mathfrak{s} + \mathfrak{C}y + \mathfrak{D}z)$$

Now we substitute $\mathfrak{r} = -\mathfrak{A}y^\star$, and add and subtract $z^T \mathfrak{C}y^\star$:

$$\dot{V}(x(t)) = \Delta y^T (-\mathfrak{A}y^\star + \mathfrak{A}y + \mathfrak{B}z) + z^T (\mathfrak{s} + \mathfrak{C}y + \mathfrak{D}z + \mathfrak{C}y^\star - \mathfrak{C}y^\star)$$
$$= \Delta y^T (\mathfrak{A}\Delta y + \mathfrak{B}z) + z^T (\mathfrak{s} + \mathfrak{C}\Delta y + \mathfrak{D}z + \mathfrak{C}y^\star)$$

Now we write the function as the sum of two parts:

$$\dot{V}(x(t)) = (\Delta y^T \mathfrak{A}\Delta y + \Delta y^T \mathfrak{B}z + z^T \mathfrak{C}\Delta y + z^T \mathfrak{D}z) + z^T (s + \mathfrak{C}y^\star)$$
$$= \begin{pmatrix} \Delta y \\ z \end{pmatrix}^T \begin{pmatrix} \mathfrak{A} & \mathfrak{B} \\ \mathfrak{C} & \mathfrak{D} \end{pmatrix} \begin{pmatrix} \Delta y \\ z \end{pmatrix} + z^T (s + \mathfrak{C}y^\star)$$

$$= \begin{pmatrix} \Delta y \\ z \end{pmatrix}^T A \begin{pmatrix} \Delta y \\ z \end{pmatrix} + z^T (s + \mathfrak{C}y^\star)$$

Whenever $H(A) = \frac{1}{2}(A + A^T)$ is negative definite, then the first term is negative for any choice of y and z. Examining the second term, we see that $\mathfrak{s} + \mathfrak{C}y^\star$ measures the invasion growth rate of the populations in the set $n - k$ when they are attempting to invade the community that is resting at $y^\star$. Thus, if we can find a saturated equilibrium, it is globally stable and will be reached for any $x(0) > 0_n$.

This derivation can be extended by considering a diagonal matrix $D(w)$ with $w > 0_n$, as done above.

1.9 Classic papers, references and further readings

A brief paper discussing how to build models in biology:

- Richard Levins, 1966. *The strategy of model building in population biology*. American Scientist 54:421-431

The Lotka-Volterra predator-prey model was discovered independently by Alfred J. Lotka and Vito Volterra:

- Alfred J. Lotka, 1920. *Analytical Note on Certain Rhythmic Relations in Organic Systems*. PNAS 6 (7) 410-415

- Vito Volterra, 1926. *Fluctuations in the Abundance of a Species Considered Mathematically*. Nature 118:558-60

You can read their exchange here.

The constant of motion that underlies the candidate Lyapunov functions was derived by Lotka in 1920:

- Alfred J. Lotka, 1920. *Undamped oscillations derived from the law of mass action*. Journal of the American Chemical Society 42:1595-1599

Volterra considered many variations, including the competition between species. His results caught the eye of an experimentalist, who validated the principle of competitive exclusion using protozoans:

- G.F. Gause, 1934. Experimental Analysis of Vito Volterra's Mathematical Theory of the Struggle for Existence. Science 79:16-17

The paper by MacArthur, on consumer-resource dynamics:

- R. MacArthur, 1970. Species packing and competitive equilibrium for many species. Theoretical population biology, 1(1), pp.1-11.

The paper by B.S. Goh on global stability:

- B.S. Goh, 1977. Global stability in many-species systems. The American Naturalist, 111(977), pp.135-143.

The convergence to saturated equilibria has strong implications for ecological assembly. See for example:

- J. Hofbauer, S.J. Schreiber, 2022. Permanence via invasion graphs: incorporating community assembly into modern coexistence theory. Journal of mathematical biology. Nov;85(5):54.

- C.A. Serván, S. Allesina, 2021. Tractable models of ecological assembly. Ecology Letters May;24(5):1029-37.

I have recently written a paper on Lyapunov functions for GLV that extends and generalizes Goh's function. Ask me about it if you want to know more!

- S. Allesina, 2025. Global stability of ecological and evolutionary dynamics via equivalence. In review

2 GLV with random parameters

2.1 All species growing logistically

Suppose we take n populations, each growing according to:

$$\dot{x}_i = x_i(r_i - A_{ii}x_i)$$

with $A_{ii} > 0$. We assume that the growth rates are sampled independently from a distribution: $r_i \sim Q$, a distribution with mean 0, $\mathbb{E}(r_i) = 0$ and symmetric about its mean, such that $\phi(r_i) = \phi(-r_i)$, where $\phi(\cdot)$ is the p.d.f. of distribution Q. For example, we could choose $r_i \sim \mathcal{N}(0, \sigma^2)$, or $r_i \sim \mathcal{U}[-1, 1]$. Naturally, whenever $r_i > 0$, the population will grow to $x_i^\star = r_i/A_{ii}$. If $r_i < 0$, on the other hand, the population will go extinct. Because of the symmetry around zero, each population has therefore probability $1/2$ of persisting. When we have n populations, the number of coexisting populations $\|k\|$ is a random variable following the binomial distribution:

$$p(\|k\| \| n) = \binom{n}{\|k\|}\frac{1}{2^n} \quad \|k\| \sim \mathcal{B}\left(n, \frac{1}{2}\right)$$

2.2 The random zoo

Now consider a GLV model with random parameters. We choose r_i from a distribution with mean zero and symmetric about the mean, and each interaction A_{ij} from a distribution with mean zero and symmetric about the mean. Moreover, we add a constant to the diagonal of the matrix such that the symmetric part of A, $H(A) = \frac{1}{2}(A + A^T)$ is positive definite. As we have seen before, this means that dynamics will always converge to a saturated equilibrium.

We now introduce a family of 2^n matrices S_i, with:

$$S_1 = \begin{pmatrix} 1 & 0 & 0 & \cdots & 0 \\ 0 & 1 & 0 & \cdots & 0 \\ 0 & 0 & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & 0 & 1 \end{pmatrix} = I_n$$

$$S_2 = \begin{pmatrix} -1 & 0 & 0 & \cdots & 0 \\ 0 & 1 & 0 & \cdots & 0 \\ 0 & 0 & 1 & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & 0 & 1 \end{pmatrix}$$

$$S_3 = \begin{pmatrix} 1 & 0 & 0 & \cdots & 0 \\ 0 & -1 & 0 & \cdots & 0 \\ 0 & 0 & 1 & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & 0 & 1 \end{pmatrix}$$

$$S_4 = \begin{pmatrix} -1 & 0 & 0 & \cdots & 0 \\ 0 & -1 & 0 & \cdots & 0 \\ 0 & 0 & 1 & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & 0 & 1 \end{pmatrix}$$

$$\vdots$$

$$S_{2^n} = \begin{pmatrix} -1 & 0 & 0 & \cdots & 0 \\ 0 & -1 & 0 & \cdots & 0 \\ 0 & 0 & -1 & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & 0 & -1 \end{pmatrix} = -I_n$$

These matrices, called *signature matrices* are their own inverse (a matrix with this property is called *involutory*), and therefore, we have that $S_i S_i = S_i^2 = I_n$. Geometrically, these matrices represent a reflection in each of the axes corresponding to the negated rows or columns.

We then consider what happens when we transform the parameters by multiplying them by S_i. Take an arbitrary GLV system, and solve for the x that makes $r + Ax = 0_n$:

$$x = -A^{-1}r$$

The vector is a feasible equilibrium for the system if $x > 0_n$. Now consider the transformed system:

$$r' = S_i r \quad A' = S_i A S_i$$

Note that A' is similar to A, and therefore has the same eigenvalues; moreover, $\phi(r') = \phi(r)$ and $\phi(A') = \phi(A)$, because of symmetry. Now compute the new solution

$$x' = -(S_i A S_i)^{-1} S_i r$$
$$= -S_i A^{-1} S_i S_i r$$
$$= -S_i A^{-1} r$$
$$= S_i x$$

That is, the transformation changes the sign of the components of x corresponding to the negative coefficients in S_i. Hence, for any possible choice of r and A, there is only one possible choice of S_i that makes the equilibrium feasible. Because all matrices A' and all vectors r' have the same probability/density, then the probability of having a positive x is exactly $1/2^n$. Thus, a system with random parameters and a strongly stable matrix of interactions has the same probability of feasibility as that of a system in which populations are not interacting!

We have seen that when A is such that $H(A)$ is negative definite, dynamics always converge to a saturated equilibrium. We want to compute the probability of finding a saturated equilibrium, in which populations belonging to set k coexist, and the remaining populations cannot invade when rare.

We thus divide x, r and A as:

$$x = \begin{pmatrix} y \\ z \end{pmatrix} \quad \tilde{x} = \begin{pmatrix} y^\star \\ 0_{\|n-k\|} \end{pmatrix} \quad A = \begin{pmatrix} \mathfrak{A} & \mathfrak{B} \\ \mathfrak{C} & \mathfrak{D} \end{pmatrix} \quad r = \begin{pmatrix} \mathfrak{r} \\ \mathfrak{s} \end{pmatrix}$$

We also divide S_i into:

$$S_i = \begin{pmatrix} S_i^{(k)} & 0_{\|k\|,\|n-k\|} \\ 0_{\|n-k\|,\|n\|} & S_i^{(n-k)} \end{pmatrix}$$

When we use the signature matrix, the vector $\mathfrak{s}$ and the matrix $\mathfrak{C}$ become:

$$\mathfrak{s}' = S_i^{(n-k)} \mathfrak{s} \quad \mathfrak{C}' = S_i^{(n-k)} \mathfrak{C} S_i^{(k)}$$

The feasibility and nonivasibility condition, for a given choice of S_i read:

$$\begin{cases} y' = S_i^{(k)}(-\mathfrak{A}^{-1}\mathfrak{r}) > 0_{\|k\|} \\ D(z)^{-1} z = S_i^{(n-k)}(\mathfrak{s} + \mathfrak{C}y') < 0_{\|n-k\|} \end{cases}$$

There is only one choice out of $2^{\|k\|}$ that makes $y' > 0_{\|k\|}$; moreover, there is only one choice of $S_i^{(n-k)}$ that fulfills the noninvasibility condition, out of $2^{\|n-k\|}$ equiprobable choices. Then, we have that the probability of finding exactly $\|k\|$ populations coexisting at the saturated equilibrium, with the remaining $\|n-k\|$ that cannot invade is exactly $1/(2^{\|k\|} \cdot 2^{\|n-k\|}) = 1/2^n$. The number of coexisting populations at the saturated equilibrium follows the binomial distribution:

$$p(\|k\| \| n) = \binom{n}{\|k\|} \frac{1}{2^n} \quad \|k\| \sim \mathcal{B}\left(n, \frac{1}{2}\right)$$

exactly as for the non-interacting case.

2.3 Random zoo and experimental data

We have seen above that in a (stable) GLV model with random interactions, the expected number of species coexisting is proportional to the size of the initial pool: $\mathbb{E}(\|k\|) = n/2$. We start the system with all the populations present, and we assemble a final community from the *top-down*. Interestingly, this type of experiment is carried out with increasing frequency in microbial ecology, where a microbial community taken from a certain environment is challenged with a new synthetic environment in the laboratory. For example, Leonora Bittleston and colleagues extracted the microbial communities inhabiting 10 distinct pitcher plants, and cultured them in synthetic media in the laboratory for two months. They plot the number of microbial strains present at the beginning of the experiment (Day 3, such that the strains that cannot grow in the medium are filtered out) and after two months (Day 63), finding a striking linear relationship between the initial size n and that at the end of the experiment $\|k\|$:
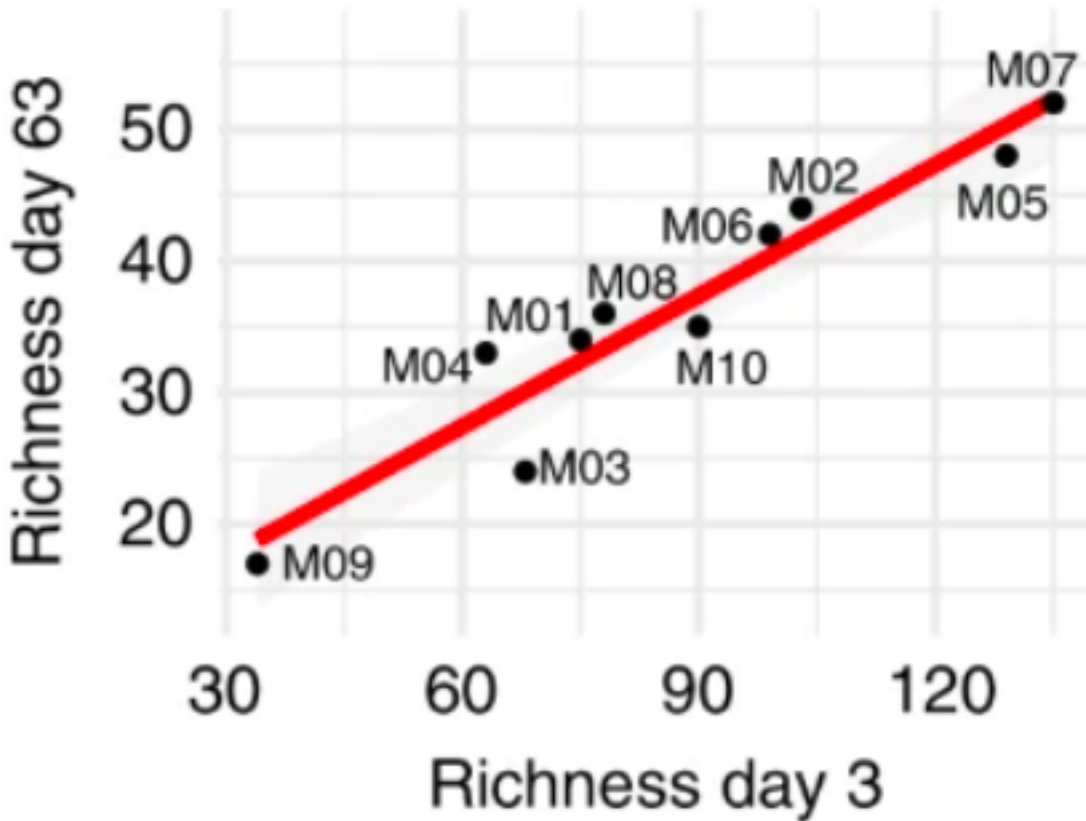
2.4 Competitive GLV

We now consider a more complicated case, in which we have a competitive GLV system:

$$\dot{x}_i = x_i r_i \left(1 - \sum_j M_{ij} x_j \right)$$

where the matrix of interactions is given by the sum of two matrices:

$$M = \alpha I + B$$

and B is a random matrix, with entries sampled independently from a distribution with mean $\mu > 0$, and unit variance. We want to calculate the probability that the system has a feasible equilibrium, and how the probability changes when we increase α.

The value of $\alpha > 0$ can be considered the "excess" intraspecific interaction in the system. To show that this value influences feasibility, we start by showing that a sufficiently large α guarantees feasibility.

2.5 Effect of average interaction strength on feasibility

We have taken $M = \alpha I + B$; call m the vector of column means of B. Here we show that, as long as $m > 0_n$, its actual value has no effect on feasibility. We can write:

$$M = \alpha I + B$$
$$= \alpha I + 1_n m^T + C$$

where C has columns summing to zero $(1_n^T C = 0_n^T)$. For feasibility, we need the solution:

$$Mx = 1_n$$
$$x = M^{-1} 1_n > 0_n$$

We consider the simpler system:

$$(\alpha I + C)y = 1_n$$
$$y = (\alpha I + C)^{-1} 1_n$$

and write the solution x as a rank-1 update of the solution of the system in y.

> **ℹ Sherman-Morrison formula**
>
> Suppose that $A + uv^T$ is invertible, where A is a $n \times n$ matrix, and u and v are column vectors of size n. The matrix is invertible as long as $1 + v^T A^{-1} u \neq 0$.
> If this is the case
>
> $$(A + uv^T)^{-1} = A^{-1} - \frac{1}{1 + v^T A^{-1} u} A^{-1} uv^T A^{-1}$$
>
> This formula is useful when we need to update the matrix inverse after a rank-1 perturbation.

Using the Sherman-Morrison formula, we obtain:

$$x = ((\alpha I + C) + 1_n m^T)^{-1} 1_n$$

$$= \left((\alpha I + C)^{-1} - \frac{1}{1 + m^T((\alpha I + C)^{-1})1_n}(\alpha I + C)^{-1}1_n m^T(\alpha I + C)^{-1} \right) 1_n$$

$$= y - \frac{1}{1 + m^T y} y m^T y$$

$$= \frac{1}{1 + m^T y} y$$

Thus, x and y are proportional to each other, with constant of proportionality $1/(1 + m^T y)$. Then $x > 0_n$ when either a) $y > 0_n$, and $1 + m^T y > 0$, or b) $y < 0_n$ and $1 + m^T y < 0$. Sum the equations in y:

$$1_n^T(\alpha I + C)y = 1_n^T 1_n$$

$$\alpha 1_n^T y = n$$

$$\frac{1}{n} 1_n^T y = \frac{1}{\alpha}$$

This means that y cannot be all negative; then given that for $y > 0_n$ and $m > 0_n$ we have $1 + m^T y > 0$, we have that x is feasible if and only if y is feasible.

This means that any matrix that can be written as $B = C + 1m^T$ with $m > 0_n$ belongs to the same class for feasibility—the exact value of $m > 0_n$ does not matter.

2.6 A sufficiently large α guarantees feasibility

We want to show that the system of equations

$$(\alpha I + C)y = 1_n$$

has a positive solution $y > 0_n$ for α large enough. To this end, we first divide both sides by $\alpha > 0$:

$$\left(I + \frac{1}{\alpha}C \right) y = \frac{1}{\alpha} 1_n$$

We have seen above that $\alpha 1_n^T y / n = 1$; we multiply the r.h.s. by this value, obtaining:

$$\left(I + \frac{1}{\alpha}C \right) y = \frac{1}{\alpha} 1_n \frac{\alpha}{n} 1_n^T y$$

$$\left(\frac{1}{\alpha}C \right) y + y = \frac{1}{n} 1_n 1_n^T y$$

$$\left(\frac{1}{n} 1_n 1_n^T - \frac{1}{\alpha}C \right) y = y$$

Thus, we have that y is a right eigenvector of matrix $\frac{1}{n} 1_n 1_n^T - \frac{1}{\alpha}C$, associated with $\lambda = 1$.

> **i** Perron-Frobenius theorem
>
> The matrix A has all coefficients positive $A_{ij} > 0 \, \forall i, j$.
> Then the matrix has a single positive real eigenvalue ρ (spectral radius, or Perron root) such that $|\lambda_i| < \rho$ for all other eigenvalues. Moreover, the eigenvalue is associated with an eigenvectors that can be made all positive (Perron eigenvector).

If we choose $\alpha = \alpha_\infty$ such that $C_{ij}/\alpha_\infty < 1/n$, then the matrix $\frac{1}{n} 1_n 1_n^T - \frac{1}{\alpha_\infty} C$ has only positive coefficients; moreover all columns sum to unity and therefore the spectral radius is $\rho = 1$. Because of Perron-Frobenius theorem, $y > 0_n$.

2.7 Models with random interactions

We have seen above that the system $(\alpha I + C)y = 1_n$, with $C^T 1_n = 0_n$ and $\alpha > 0$ has solution y with mean $\frac{1}{n} 1_n^T y = \frac{1}{\alpha}$. If the populations are *statistically equivalent*, i.e., there is no special structure making some of the populations necessarily different from the rest, we can generalize this further:

$$\left(\sum_j y_j \right)^2 = \frac{n^2}{\alpha^2}$$

$$\sum_j (y_j)^2 + \sum_i \sum_{j \neq i} y_i y_j = \frac{n^2}{\alpha^2}$$

$$n\mathbb{E}((y_i)^2) + n(n-1)\mathbb{E}(y_i y_j) = \frac{n^2}{\alpha^2}$$

$$\mathbb{V}(y_i) + \mathbb{E}(y_i)^2 + (n-1)\left(\mathbb{Cov}(y_i, y_j) + \mathbb{E}(y_i)\mathbb{E}(y_j) \right) = n\mathbb{E}(y_i)^2$$

$$\mathbb{V}(y_i) + \mathbb{E}(y_i)^2 + (n-1)\left(\mathbb{Cov}(y_i, y_j) + \mathbb{E}(y_i)^2 \right) = n\mathbb{E}(y_i)^2$$

$$\mathbb{V}(y_i) + (n-1)\mathbb{Cov}(y_i, y_j) = 0 \quad ,$$

where we have exploited the fact that, for a model with statistically equivalent populations, $\mathbb{E}(y_i)\mathbb{E}(y_j) = \mathbb{E}(y_i)^2$, and that the covariance $\mathbb{Cov}(y_i, y_j)$ must be the same for all i, j. Thus, for *any* unstructured model, we have that the expected covariance is negative. Moreover, for a given variance $\mathbb{V}(y_i) = \sigma_y^2$, we have: $\sigma_y^2 + (n-1)\sigma_y^2 \mathbb{Cor}(y_i, y_j) = 0$ and thus $\mathbb{Cor}(y_i, y_j) = -1/(n-1)$ for all i and j. Note that this is the maximally negative correlation one can have for equicorrelated random variables. Thus, y has expectation $(1/\alpha)1_n$, and covariance matrix $\sigma_y^2 \left(\frac{n}{n-1} I - \frac{1}{n-1} 1_n 1_n^T \right)$. Importantly, the only difference between different unstructured models with random parameters is the value of σ_y^2, while the rest is unchanged. Analyzing increasingly complex models therefore reduces to the problem of determining the variance of y.

2.8 Approximating feasibility

The joint distribution of y is well-approximated by a multivariate normal in the limit of large n, because of the central limit theorem.

Therefore, y is asymptotically distributed as

$$y \sim \mathcal{N}\left(\frac{1}{\alpha}\mathbb{1}_n, \sigma_y^2\left(\frac{n}{n-1}I - \frac{1}{n-1}\mathbb{1}_n\mathbb{1}_n^T\right)\right) \quad .$$

Because the joint distribution of y is well-approximated by a multivariate normal, we can calculate the probability of feasibility as a function of α, n, as well as σ_y^2 by integrating the probability density function in the positive orthant of $\mathbb{R}^n$—what is called an "orthant probability":

$$p_F(n, \alpha, \sigma_y^2) = \int_0^\infty \int_0^\infty \cdots \int_0^\infty \phi(y)dy_1 dy_2 \cdots dy_n \quad ,$$

where $\phi(y)$ is the probability density function of the normal distribution above. For equicorrelated random variables, the multiple integral above can be reduced to a single integral (albeit involving complex variables when the correlation is negative, such as in this case). Equivalently, one can use the theory of order statistics to write the density function of the first order statistics (i.e., the $\min_i(y_1, y_2, \dots, y_n)$) and integrate this density function for all positive values of the minimum.

When n is large, however, one can safely ignore the negative correlation between the random variables y_i, and pretend they are independent. In this case, we want to determine the probability that all $y_i > 0$. If we subtract the mean from both sides, and call $\zeta_i = y_i - 1/\alpha$, we have that the system is feasible when all $\zeta_i > -1/\alpha$. Dividing both sides by σ_y and calling $\xi_i = \zeta_i/\sigma_y$ we have that feasibility is ensured whenever all the ξ_i, following the standard normal distribution, are larger than $-1/(\alpha\sigma_y)$; because the standard normal is symmetric about zero, we can finally write:

$$p_F(n, \alpha, \sigma_y^2) \approx \Phi\left(\frac{1}{\alpha\sigma_y}\right)^n \quad ,$$

where $\Phi(\cdot)$ is the cumulative distribution function for a standard normal distribution. The approximation is going to be accurate when n is large. Again, we have reduced the problem of computing the probability of feasibility for a system of a known size n and given level of self-regulation α to the problem of computing σ_y for the specific model and parameters.

ℹ Neumann series

If the matrix T has spectral radius $\rho(A) < 1$ (i.e., the maximum absolute value of its eigenvalues is less than one), then we can write the inverse

$$(I - T)^{-1} = \sum_{k=0}^\infty T^k$$

Where $T^0 = I$.

We have

$$(\alpha I + C)y = 1_n$$

$$\left(I + \frac{1}{\alpha}C\right)y = \frac{1}{\alpha}1_n$$

$$y = \frac{1}{\alpha}\left(I + \frac{1}{\alpha}C\right)^{-1}1_n$$

$$y = \frac{1}{\alpha}\sum_l\left(-\frac{1}{\alpha}C\right)^l 1_n$$

$$y \approx \frac{1}{\alpha}\left(1_n - \frac{1}{\alpha}C1_n + \frac{1}{\alpha^2}C^21_n + \cdots\right)$$

Taking only the first two terms, and computing the variance, we obtain:

$$\sigma_y^2 = E(y^2) - E(y)^2$$

$$= \frac{1}{n}y^Ty - \frac{1}{\alpha^2}$$

$$\approx \frac{1}{n\alpha^2}(1_n - \frac{1}{\alpha}C1_n)^T(1_n - \frac{1}{\alpha}C1_n) - \frac{1}{\alpha^2}$$

$$\approx \frac{1}{n\alpha^2}(1_n^T1_n - \frac{1}{\alpha}1_n^TC^T1_n - \frac{1}{\alpha}1_n^TC1_n + \frac{1}{\alpha^2}1_n^TC^TC1_n) - \frac{1}{\alpha^2}$$

$$\approx \frac{1}{n\alpha^2}(n - 0 - 0 + \frac{1}{\alpha^2}1_n^TC^TC1_n) - \frac{1}{\alpha^2}$$

$$\approx \frac{1}{n\alpha^4}1_n^TC^TC1_n$$

Suppose that $B_{ij} \sim \mathcal{N}(0,1)$ then, plugging in $C = B - 1_n m^T$, with $B^T 1_n = nm$ we obtain:

$$\sigma_y^2 \approx \frac{1}{n\alpha^4}1_n^T(B^T - m1_n^T)(B - 1_n m^T)1_n$$

$$\approx \frac{1}{n\alpha^4}1_n^T\left(B^TB - m1_n^TB - B^T1_n m^T + m1_n^T1_n m^T\right)1_n$$

$$\approx \frac{1}{n\alpha^4}1_n^T\left(B^TB - nmm^T - nmm^T + nmm^T\right)1_n$$

$$\approx \frac{1}{n\alpha^4}\left(1_n^TB^TB1_n - n1_n^Tmm^T1_n\right)$$

Finally, we take expectations of both terms:

$$\mathbb{E}(1_n^TB^TB1_n) = \mathbb{E}\left(\sum_i\left(\sum_j B_{ij}\right)^2\right) = n^2$$

$$\mathbb{E}((m^T1_n)^2) = \mathbb{E}\left(\left(\frac{1}{n}\sum_{ij}B_{ij}\right)^2\right) = \frac{1}{n^2}\mathbb{E}\left(\left(\sum_{ij}B_{ij}\right)^2\right) = 1$$

Putting them together, we obtain:

$$\mathbb{E}(\sigma_y^2) \approx \frac{1}{n\alpha^4}(n^2 - n) = \frac{n-1}{\alpha^4}$$

Which gives us a reasonable approximation for the probability of feasibility. For example, we compute numerically the probability that a system of size $n = 250$ is feasible for different values of α:

2.9 A more accurate approximation of feasibility

Expanding the Neumann series even further, or using a different technique based on resolvents, we find a better approximation for the σ_y^2:

$$\mathbb{E}(\sigma_y^2) \approx \frac{n-1}{\alpha^4 - (n-1)\alpha^2}$$

The analysis can also be extended to more complicated cases in which the entries in B are correlated.

2.10 Only equilibria

For matrices with random entries, it is easy to calculate the value of α that would be needed to have $H(\alpha I + B)$ positive definite (such that any feasible equilibrium would be globally stable). In particular, if $B_{ij} \sim \mathcal{N}(\mu, \sigma^2)$, the eigenvalues of B are contained in a circle in the complex plane (circular law), with radius $\sqrt{n\sigma^2}$, plus a single, real outlier at approximately $n\mu$. If we add the matrix αI, all the eigenvalues are shifted of α.

The eigenvalues of $H(\alpha I + B) = \alpha I + \frac{1}{2}(B + B^T)$ are all real (because the matrix is symmetric). The entries of $(B_{ij} + B_{ji})/2$ are normally distributed, with mean μ and variance $\sigma^2/2$ (because the variances add up, and dividing all the entries by 2 divides the variance by 4).

The bulk of the eigenvalues are approximately distributed according to Wigner's semicircle law:

$$\phi(\lambda) = \frac{2}{\pi R^2}\sqrt{R^2 - \lambda^2}$$

where in this case $R = \sqrt{2n\sigma^2}$

and with an eigenvalue at $n\mu$. For stability, we need therefore to have $\alpha > \sqrt{2n}$. What is the probability of feasibility at this value of α?

Thus, for large competitive systems of this type, feasibility typically implies stability. But given that coexistence requires a feasible equilibrium, this means that in these systems dynamics will always converge to a globally stable saturated equilibrium, and we will never observe cycles or chaos.

2.11 References and further readings

Coexistence in GLV with random parameters and stable interaction matrix

- Serván, C.A., Capitán, J.A., Grilli, J., Morrison, K.E. and Allesina, S., 2018. Coexistence of many species in random ecosystems. Nature ecology & evolution, 2(8), pp.1237-1242.

Experiment on pitcher plant microbial communities

- Bittleston, L.S., Gralka, M., Leventhal, G.E., Mizrahi, I. and Cordero, O.X., 2020. Context-dependent dynamics lead to the assembly of functionally distinct microbial communities. Nature communications, 11(1), p.1440.

On the existence of chaos in competitive GLV

- Smale, S., 1976. On the differential equations of species in competition. Journal of Mathematical Biology, 3(1), pp.5-7.
- Vano, J.A., Wildenberg, J.C., Anderson, M.B., Noel, J.K. and Sprott, J.C., 2006. Chaos in low-dimensional Lotka–Volterra models of competition. Nonlinearity, 19(10), p.2391.

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- Bizeul, P. and Najim, J., 2021. Positive solutions for large random linear systems. Proceedings of the American Mathematical Society, 149(6), pp.2333-2348.

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3 GLV and experimental data

3.1 Experiments in which different combinations of species are grown together

For this exploration, we are going to consider a popular type of experiment in which different combinations of species, taken from a *species' pool* are co-cultured.

These experiments are routinely conducted with plants (for example, to test the relationship between productivity and biodiversity), bacteria (for example, to determine rules of thumb for coexistence), protozoans, etc.

In many cases, only the final outcome (i.e., the density of the populations at the end of each experiment) is available/recorded.

Typically, the pool of species to experiment with contains only species that can grow in isolation.

If one has access to a pool of n species, testing all the possible $2^n - 1$ combinations obtained by including/excluding each of the species rapidly becomes impractical as n grows. Therefore, all the possible combinations are tested only when n is small, while a small fraction of the possible communities is typically available when n is large.

3.2 Example data

For our explorations, we are going to use recent data from Ishizawa and colleagues, which you can find here:

H. Ishizawa, Y. Tashiro, D. Inoue, M. Ike, H. Futamata. *Learning beyond-pairwise interactions enables the bottom–up prediction of microbial community structure* PNAS 121 (7) e2312396121 (2024).

The Authors inoculated duckweed (*Lemna minor*) with synthetic bacterial communities formed by all possible combinations of seven strains. To this end, they cultured the infected duckweed in flasks for 10 days. At the end of the experiment, they plated the communities on agar plates containing antibiotics that would allow the growth only of a particular strain. In this way, they were able to measure the final density of each of the seven strains in each of the $2^7 - 1 = 127$ possible communities, and conducted each experiment in replicate. The full data set reports the outcome of 692 separate experiments!

More modestly, here we are going to focus on a smaller pool of three strains taken from the seven available. We therefore have 7 possible communities, ranging from a single strain growing in isolation to the three strains growing together. For example, a few of the measurements are:

We can therefore associated each measurement with a) the strain being measured, i; b) the community in which i was grown, k; and c) the (biological) replicate experiment, r.

3.3 A simple statistical framework

The simplest model we can write for this type of data is one in which the outcomes of replicate experiments are independent samples from a distribution:

$$\tilde{x}_i^{(k,r)} \sim Q_i \left(x_i^{(k)}, \gamma_i^{(k)} \right)$$

where $\tilde{x}_i^{(k,r)}$ is the *observed* density of population i for the r replicate in which population i is grown in community k. The value $x_i^{(k)}$ represents the *true* mean of the distribution (i.e., the average if we were to conduct many replicates—hence it does not depend on r), and $\gamma_i^{(k)}$ is a parameter (or several parameters) controlling the shape of the distribution Q_i.

Implicitly, we are making a very strong assumption: if we observe the community k, it is always found around $x^{(k)}$—i.e., we cannot have *true multistability*, in which, depending on initial conditions, we end up with different outcomes in which all populations are present (we can still have that, depending on initial condition, the system ends up at different points/attractor, as long as they have different compositions).

This model requires estimating all the $x_i^{(k)}$ and $\gamma_i^{(k)}$, and is therefore not very useful. To make the model applicable to real data, we make another strong assumption:

$$x_i^{(k)} = \alpha_i - \sum_{j \in k;\ j \neq i} \beta_{ij} x_j^{(k)}$$

The interpretation is simple: if population i is grown by itself, it will reach the carrying capacity α_i; if other species are co-cultured along with i, they will change the final density of i according to their density $(x_j^{(k)})$ and an interaction term β_{ij}.

We perform some manipulations:

$$\sum_{j \in k;\ j \neq i} \beta_{ij} x_j^{(k)} + x_i^{(k)} = \alpha_i$$

$$\sum_{j \in k;\ j \neq i} \frac{\beta_{ij}}{\alpha_i} x_j^{(k)} + \frac{1}{\alpha_i} x_i^{(k)} = 1$$

$$\sum_{j \in k;\ j \neq i} B_{ij} x_j^{(k)} + B_{ii} x_i^{(k)} = 1$$

$$\sum_{j \in k} B_{ij} x_j^{(k)} = 1$$

$$\left(B^{(k,k)} x^{(k)} \right)_i = 1$$

$$B^{(k,k)} x^{(k)} = 1_{\|k\|}$$

But this is exactly the structure of the equilibria for a GLV model, which we have introduced in Lecture 1.

3.4 The structure of equilibria in GLV

Take the model:

$$\dot{x} = D(x \circ r)(1_n - Bx)$$

with $r > 0_n$; compute all the feasible equilibria and collect them into a matrix E. For example:

$$B = \begin{pmatrix} 2 & -3 & 3 \\ -2 & 7 & -3 \\ 2 & -2 & 2 \end{pmatrix} \qquad E = \begin{pmatrix} \frac{1}{2} & 0 & 0 \\ 0 & \frac{1}{7} & 0 \\ 0 & 0 & \frac{1}{2} \\ \frac{5}{4} & \frac{1}{2} & 0 \\ 0 & \frac{5}{8} & \frac{9}{8} \\ \frac{1}{2} & \frac{1}{2} & \frac{1}{2} \end{pmatrix}$$

where each row contains a feasible equilibrium (if it exists) corresponding to a given composition.

Consider the matrix:

$$1_m 1_n^T - EB^T = \begin{pmatrix} 0 & 2 & 0 \\ \frac{10}{7} & 0 & \frac{9}{7} \\ -\frac{1}{2} & \frac{5}{2} & 0 \\ 0 & 0 & -\frac{1}{2} \\ -\frac{1}{2} & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}$$

For each row, we find 0 for the corresponding population at equilibrium (in red), and the remaining values express $(1_n - Bx^{(k)})_j$, which has the same sign as the invasion growth rates for population j, when $r > 0_n$. Hence, a saturated equilibrium will correspond to a row with nonpositive values (e.g., the community $k = \{1, 2\}$ is saturated, because population 3 cannot invade when rare).

Next, call E_i the submatrix obtained selecting only rows for which $x_i^{(k)} > 0$. For example, for population 1:

$$E_1 = \begin{pmatrix} \frac{1}{2} & 0 & 0 \\ \frac{5}{4} & \frac{1}{2} & 0 \\ \frac{1}{2} & \frac{1}{2} & \frac{1}{2} \end{pmatrix}$$

We have that:

$$E_i B_i = 1_l$$

Where B_i is the ith row of B, and l is the number of experiments in which i is present:

$$E_1 B_1 = \begin{pmatrix} \frac{1}{2} & 0 & 0 \\ \frac{5}{4} & \frac{1}{2} & 0 \\ \frac{1}{2} & \frac{1}{2} & \frac{1}{2} \end{pmatrix} \begin{pmatrix} 2 \\ -3 \\ 3 \end{pmatrix} = \begin{pmatrix} 1 \\ 1 \\ 1 \end{pmatrix}$$

Practically, this means that all the ith component of all the equilibria $x^{(k)}$ of a GLV model belong to a *hyperplane* in $\mathbb{R}^n$ defined by $\sum_j B_{ij} x_j^{(k)} = 1$.

This also means that we can recover the values of B_i from the equilibria:

$$B_i = E_i^{-1} 1_n$$

which can be computed when E_i is square. Otherwise, use the Moore-Penrose pseudo-inverse. For example:

$$E_2 = \begin{pmatrix} 0 & \frac{1}{7} & 0 \\ \frac{5}{4} & \frac{1}{2} & 0 \\ 0 & \frac{5}{8} & \frac{9}{8} \\ \frac{1}{2} & \frac{1}{2} & \frac{1}{2} \end{pmatrix}$$

$$(E_2^T E_2)^{-1} E_2^T 1_4 = \begin{pmatrix} -2 \\ 7 \\ -3 \end{pmatrix} = B_2$$

This also provides a naive method to get a draft of B when only the equilibrium values are available.

The method is going to return a unique solution provided that each matrix E_i has rank n. In practice, this means that, for each population i, a) E_i has at least n rows (i.e., population i is present at n distinct equilibria), and b) each species j is present in at least one equilibrium with i, i.e., each pair of populations is found in at least one equilibrium.

This might be a tall order when n is large, and in the tutorial we will see how to circumvent this issue.

3.5 Predicting coexistence

Suppose that we have estimated the matrix B, and that we want to determine whether a certain combination of populations can or cannot coexist. This is useful when we have sufficient data to estimate B, but we have not carried out all the possible experiments—we want to predict the outcome of further experiments in advance.

Then, according to our statistical model, we can take $B^{(k,k)}$ for the desired community k, and take the row sums of the inverse:

$$x^{(k)} = \left(B^{(k,k)}\right)^{-1} 1_{\|k\|}$$

If all the components of $x^{(k)}$ are positive, we assume that this will be the outcome of the experiment. If *any* of the components is negative, on the other hand, we conclude that the populations cannot coexist.

3.6 Scoring matrices B

The paragraph above suggests a good way to score matrices in practice (i.e., when the empirically-observed matrix $\tilde{E}$ is a noisy estimate of a true matrix E):

- Propose a matrix B
- Compute $x^{(k)}$ for each observed $\tilde{x}^{(k,r)}$
- Try to minimize the *distance* between the predicted and observed

Naturally, this algorithm relies on a notion of distance. The simplest choice would be to choose B such that the sum of squared deviations is minimized:

$$SSQ(B) = \sum_r \sum_k \sum_i \left(\tilde{x}_i^{(k,r)} - x_i^{(k)}\right)^2$$

When the values of $\tilde{x}_i^{(k)}$ vary considerably (as expected when populations interact), minimizing the SSQ will favor matrices that match closely the rows of $\tilde{E}$ containing large values, such that a 10% error on a small value of $\tilde{x}_i^{(k)}$ "counts" less than a 1% error for a large value.

If we want to put all rows on the same footing, we can implement a Weighted Least Squares scheme, in which

$$WLS(B) = \sum_r \sum_k \sum_i \left(\frac{\tilde{x}_i^{(k,r)} - x_i^{(k)}}{\sigma_i^{(k)}} \right)^2$$

where deviations are weighted by the respective standard deviation (for simplicity, we can take $\sigma_i^{(k)} = \sqrt{\mathbb{E}\left((\tilde{x}_i^{(k,r)})^2 \right) - \left(\mathbb{E}\left(\tilde{x}_i^{(k,r)} \right) \right)^2}$.

Finally, we can have a likelihood-based approach in which we are trying to maximize the sum of log-likelihoods:

$$\mathcal{L}(B) = \sum_r \sum_k \sum_i \log P\left(\tilde{x}_i^{(k,r)} | x_i^{(k)}, \gamma_i^{(k)} \right)$$

where $P(x|\mu, \gamma)$ is the density of a probability distribution function whose shape is controlled by parameters μ and γ.

In the tutorial, we are going to experiment with all three approaches, and discuss pros and cons.

3.7 References and further readings

The backbone of the statistical model can be found in numerous articles, which converged to the same solution starting from different angles:

- Xiao, Y., Angulo, M. T., Friedman, J., Waldor, M. K., Weiss, S. T., & Liu, Y.-Y. (2017). Mapping the ecological networks of microbial communities. Nature Communications, 8(1), 1–12.

- Fort, H. (2018). On predicting species yields in multispecies communities: Quantifying the accuracy of the linear Lotka-Volterra generalized model. Ecological Modelling, 387, 154–162.

- Maynard, D. S., Miller, Z. R., & Allesina, S. (2020). Predicting coexistence in experimental ecological communities. Nature Ecology & Evolution, 4(1), 91–100.

- Ansari, A. F., Reddy, Y., Raut, J., & Dixit, N. M. (2021). An efficient and scalable top-down method for predicting structures of microbial communities. Nature Computational Science, 1(9), 619–628.

- Davis, J.D., Olivença, D.V., Brown, S.P. and Voit, E.O., (2022). Methods of quantifying interactions among populations using Lotka-Volterra models. Frontiers in Systems Biology, 2, p.1021897.

For the tutorial, we are going to closely follow:

- Skwara, A., Lemos-Costa, P., Miller, Z.R. and Allesina, S., 2023. Modelling ecological communities when composition is manipulated experimentally. Methods in Ecology and Evolution, 14(2), pp.696-707.

The same method can be extended to provide a simple test for phylogenetic effects on competition/growth:

- Lemos-Costa, P., Miller, Z.R. and Allesina, S., 2024. Phylogeny structures species' interactions in experimental ecological communities. Ecology Letters, 27(8), p.e14490.

4 GLV and metatpopulation dynamics
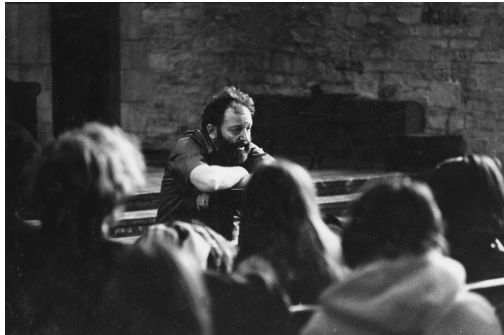
Richard Levins (1930-2016). Born in Brooklyn, New York, he studied agriculture and mathematics at Cornell. Early on, influenced by geneticist and polymath JBS Haldane, he became a Marxist activist. Upon graduation, having been blacklisted as a communist (and with the Korean War raging), he moved to Puerto Rico with his wife, and set up a farm. In his spare time, he conducted experiments on fruit flies, organized anti-colonialist rallies and anti-war protests, and taught at the University of Puerto Rico. In 1964, he was invited to Cuba to help organize the biology department of the University of Havana. He received his doctorate from Columbia University in 1965. In 1967 he moved to the University of Chicago, where he joined Richard Lewontin—with whom he established a lifelong collaboration. They both moved to Harvard in the late 1970s.

It is impossible to summarize his numerous contributions to ecology, mathematics, political science, and the philosophy of science. He has inspired countless ecologists, and his approach and style are still visible in many of the research programs being carried out today. Of particular interest for this class, his theory of evolution in a changing environment (Levins (1968)), the development of the idea of limiting similarity (MacArthur and Levins (1967)), his work on metapopulation dynamics (Levins (1969)), and the development of Loop Analysis (i.e., a qualitative theory for dynamical systems, Puccia and Levins (2013)).

4.1 Metapopulations

In 1969, Richard Levins—then a professor at U. Chicago—proposed a simple model for a "metapopulation", i.e., a "population of populations in which local extinctions are balanced by remigration from other populations" (Levins (1969)).

The model is very simple. Suppose that there are very many patches of suitable habitat, and that we track the proportion of patches occupied by a certain species, $p(t)$. Two processes affect the proportion of occupied patches: extinction, turning an occupied patch into a vacant patch, and colonization, turning a vacant patch into an occupied patch. For the simplest case, suppose that occupied patches can send "propagules" to empty patches at a fixed rate $\gamma > 0$, and that the rate at which local populations go extinct is the same for all patches, $\delta > 0$.

Call $q(t) = 1 - p(t)$ the proportion of vacant patches. Then, the dynamics are described by the equations:

$$\begin{cases} \dot{p}(t) = -\delta p(t) + \gamma p(t) q(t) \\ \dot{q}(t) = \delta p(t) - \gamma p(t) q(t) \end{cases}$$

in which we assume mass-action (like in GLV). Note that the two equations sum to zero (i.e., we're in a zero-sum setting), and therefore we can substitute $q(t) = 1 - p(t)$ to obtain:

$$\dot{p} = p(-\delta + \gamma q) = p(\gamma - \delta - \gamma p)$$

which is the usual equation for the logistic growth, with growth rate $\gamma - \delta$ and self-interaction γ. As such, as long as $\gamma > \delta$, the proportion of inhabited patches will converge to $p^\star = 1 - \delta/\gamma > 0$, which is globally stable.

4.2 Colonization-competition tradeoff

Levins' model was extended in a number of ways. One of the most interesting cases is that in which we have n species, each characterized by an extinction and a colonization rate, and there is a trade-off such that better colonizers are worse competitors, and vice versa. In particular:

- p_i is the proportion of patches occupied by population i, with $\sum_j p_j \leq 1$
- m_i is the extinction rate for population i
- c_i is the colonization rate for population i
- each species can colonize patches occupied by inferior competitors (i.e., these patches "look" empty to them)
- competitive abilities are inversely related to the colonization rates, i.e., if $c_j < c_i$, then j is a better competitor than i

The model is a system of n coupled differential equations:

$$\dot{p}_i = -m_i p_i - \sum_{j=1}^{i-1} c_j p_j p_i + c_i p_i \left(1 - \sum_{j=1}^{i} p_j \right)$$

There are three processes at play:

- $m_i p_i$ the rate at which patches occupied by i become empty
- $c_j p_j p_i$ propagules from superior competitors j (produced at rate $c_j p_j$) reach patches occupied by $i < j$ and turn them over
- propagules of i, produced at rate $c_i p_i$, reach patches that are either empty or occupied by inferior competitors (written as the difference between 1 and the sum of the proportion of patches occupied by species with equal or better competitive abilities, $1 - \sum_{j=1}^{i} p_j$) and colonize them

4.3 The model is GLV

With some rearranging, we can write this model as GLV:

$$
\begin{aligned}
\dot{p}_i &= p_i \left(-m_i - \sum_{j=1}^{i-1} c_j p_j + c_i \left(1 - \sum_{j=1}^{i} p_j \right) \right) \\
&= p_i \left(-m_i - \sum_{j=1}^{i-1} c_j p_j + c_i - c_i p_i - \sum_{j=1}^{i-1} c_i p_j \right) \\
&= p_i \left(c_i - m_i - c_i p_i - \sum_{j=1}^{i-1} (c_i + c_j) p_j \right) \\
&= p_i \left(r_i - \sum_{j} A_{ij} p_j \right)
\end{aligned}
$$

Where we have defined the matrix A:

$$
A = \begin{pmatrix}
c_1 & 0 & 0 & \cdots & 0 \\
c_1 + c_2 & c_2 & 0 & \cdots & 0 \\
c_1 + c_3 & c_2 + c_3 & c_3 & \cdots & 0 \\
\vdots & \vdots & \vdots & \ddots & \vdots \\
c_1 + c_n & c_2 + c_n & c_3 + c_n & \cdots & c_n
\end{pmatrix}
$$

and $r_i = c_i - m_i$.

We want to show that for each initial set of species in the system, dynamics will converge to a unique saturated equilibrium. To prove this, it is sufficient to find a positive diagonal matrix, $D(w)$ such that

$$
M = D(w)A + A^T D(w)
$$

is positive definite. Take $w = c^{-1}$ (i.e., the reciprocals of the colonization rates). Then we have that

$$
M = 1_n 1_n^T + Q
$$

Where

$$
Q_{ij} = \begin{cases}
1 & \text{if } j = i \\
\frac{c_i}{c_j} & \text{if } j > i \\
\frac{c_j}{c_i} & \text{if } j < i
\end{cases}
$$

To show that M is positive definite, we write the Cholesky decomposition of Q

$$
Q = R^T R
$$

With

$$R_{ij} = \begin{cases} \frac{\sqrt{c_i^2 - c_{i-1}^2}}{c_j} & \text{if } j \geq i \\ 0 & \text{if } j < i \end{cases}$$

(defining $c_0 = 0$). Note that all the elements of $R_{ij} \geq 0$. As such, Q is positive (semi-)definite, and M is the sum of two positive (semi-)definite matrices, and is thus positive (semi-)definite.

An example. Suppose $n = 3$, then:

$$A = \begin{pmatrix} c_1 & 0 & 0 \\ c_1 + c_2 & c_2 & 0 \\ c_1 + c_3 & c_2 + c_3 & c_3 \end{pmatrix}$$

$$M = D(c)^{-1}A + A^T D(c)^{-1} = \begin{pmatrix} 2 & 1 + \frac{c_1}{c_2} & 1 + \frac{c_1}{c_3} \\ 1 + \frac{c_1}{c_2} & 2 & 1 + \frac{c_2}{c_3} \\ 1 + \frac{c_1}{c_3} & 1 + \frac{c_2}{c_3} & 2 \end{pmatrix}$$

$$Q = \begin{pmatrix} 1 & \frac{c_1}{c_2} & \frac{c_1}{c_3} \\ \frac{c_1}{c_2} & 1 & \frac{c_2}{c_3} \\ \frac{c_1}{c_3} & \frac{c_2}{c_3} & 1 \end{pmatrix}$$

$$R = \begin{pmatrix} 1 & \frac{c_1}{c_2} & \frac{c_1}{c_3} \\ 0 & \frac{\sqrt{c_2^2 - c_1^2}}{c_2} & \frac{\sqrt{c_2^2 - c_1^2}}{c_3} \\ 0 & 0 & \frac{\sqrt{c_3^2 - c_2^2}}{c_3} \end{pmatrix} \qquad Q = R^T R$$

4.4 Computing equilibria

For simplicity, we are going to consider the case in which $m_i = m$ for all i. Because the matrix is lower-triangular, computing the equilibrium is especially simple, given that the equilibrium value for each species depends only on those of the preceding species. The equilibrium of the first species is given by:

$$c_1 p_1 = c_1 - m$$

and thus

$$p_1^\star = \frac{c_1 - m}{c_1} = 1 - \frac{m}{c_1}$$

The first species follows the Levins' model, and persists as long as $c_1 > m$. We compute the equilibrium for the second species, assuming that the first species is present:

$$(c_1 + c_2)p_1^\star + c_2 p_2^\star = c_2 - m$$

$$(c_1 + c_2)\left(1 - \frac{m}{c_1}\right) + c_2 p_2^\star = c_2 - m$$

$$c_1 + c_2 - m - m\frac{c_2}{c_1} + c_2 p_2^\star = c_2 - m$$

$$p_2^\star = \frac{m}{c_1} - \frac{c_1}{c_2}$$

Thus, species 2 can establish if:

$$c_2 > \frac{c_1^2}{m}$$

Computing the equilibrium of the third species we find that it is positive if:

$$c_3 > \frac{c_2^2}{\frac{c_1^2}{m}}$$

You can see that there is a simple pattern. Call $l_0 = m$, then the condition for the first species to persist is that $c_1 > l_0$; second species to persist whenever $c_2 > c_1^2/l_0 = l_1$; the third species persists whenever $c_3 > c_2^2/l_1$, and so forth:

$$l_i = \frac{c_i^2}{l_{i-1}}$$

This value represents the "shadow" each species that establishes casts on the colonization axis. A worse competitor $i + 1$ can establish if and only if:

$$c_{i+1} > l_i$$

Thus, if the species has a sufficiently large colonization rate, it will establish; if not, it will go extinct. In this way, we can compute the set of coexisting species in *linear time* (i.e., without the need to invert the matrix).

4.5 Random parameters

Sample the colonization rate values indipendently from a distribution (with positive support); for example $\gamma_i \sim \mathcal{U}[m, 1 + m]$, or from the exponential distribution $\gamma_i \sim \mathcal{E}xp(\lambda) + m$ (we sample values above the mortality rate—any lower value for the colonization rate would lead to extinction). Then sort them and assign the smallest value to species 1 ($c_1 = \min_i \gamma_i$), the second smallest value to species 2, etc. These are called the *order statistics* of the distribution.

How many species will coexist? Given that the final set of coexisting species can be found in linear time, we can run large experiments in which we compute the number of coexisting species $\|k\|$ when starting with n for different sizes n and choice of distribution from which to sample the colonization rates.

We can see that as n increases, the distribution of $\|k\|$ approaches the binomial distribution (plotted in red)—to be precise, given that the first species persists by definition (because $c_1 > m$ by design), we have that asymptotically $\|k\| - 1 \sim \mathcal{B}(n-1, \frac{1}{2})$, irrespective of the distribution used to sample the colonization rates. Therefore, as $n \to \infty$, the distribution of surviving species is *universal*.

4.6 Sketch of the proof

The argument to support these claims is a little too complicated for the time that we have available. To give a sense of how the argument is developed, we show that the probability that $\|k\| = 1$ is about $1/2^{(n-1)}$ when we sample the colonization rates from the uniform distribution $\mathcal{U}[m, m+1]$.

We can write the joint distribution for (c_1, c_n) (i.e., the smallest and largest colonization rate) for an arbitrary (absolutely continuous) distribution, from which we extract n colonization rates as:

$$f(c_1, c_n) = n(n-1)(\Phi(c_n) - \Phi(c_1))^{(n-2)}\phi(c_1)\phi(c_n)$$

where $\phi(\cdot)$ is the probability density function for the distribution used to sample the values, and $\Phi(\cdot)$ the cumulative density function.

When n is large, we can approximate the "niche shadow" value as follows. We know that species j is excluded if $c_i < c_j < l_i$, where l_i is the niche shadow cast by species i:

$$l_i = \frac{c_i^2}{l_{i-1}}$$

Thus, to be included in the set of coexisting species, we need $c_j > l_i$. We introduce X_i, the amount by which c_j exceeds l_{i-1}:

$$X_i = c_i - l_{i-1}$$

Then, we have

$$l_i = \frac{(l_{i-1} + X_i)^2}{l_{i-1}} = l_{i-1} + 2X_i + \frac{X_i^2}{l_{i-1}} \approx l_{i-1} + 2X_i = 2c_i - l_{i-1}$$

where we have neglected the term X_i^2/l_{i-1}, which is small when n is large (because the colonization values are closer together).

We now can compute the probability that species 1 excludes all other species, assuming that the niche shadow cast by species 1 is $\approx 2c_1 - m$. We need to distinguish between two cases: a) the shadow cast by species 1 does not exceed the upper bound for the distribution ($m+1$ in this case) and all other colonization rates fall into $(c_1, 2c_1 - m)$, and b) the shadow cast by species 1 exceeds the bound, and thus all other species are excluded by definition.

The niche shadow for the first species, $l_1 \approx 2c_1 - m$ does not exceed $m+1$ whenever $c_1 \leq m + 1/2$. We thus compute the probability that i) $c_1 \leq m + 1/2$, and ii) $c_n \leq 2c_1 - m$ for the uniform distribution, using:

$$\phi(z) = 1 \quad \Phi(z) = z - m$$

The density for (c_1, c_n) simplifies to:

$$f(c_1, c_n) = n(n-1)(c_n - c_1)^{(n-2)}$$

and we need to integrate this function for:

$$n(n-1) \int_m^{m+1/2} \int_{c_1}^{2c_1-m} (c_n - c_1)^{(n-2)} dc_1 dc_n = 2^{-n}$$

Now we treat the case in which c_1 exceeds $m + 1/2$, and $c_1 \le c_n \le m + 1$:

$$n(n-1) \int_{m+1/2}^{m+1} \int_{c_1}^{m+1} (c_n - c_1)^{(n-2)} dc_1 dc_n = 2^{-n}$$

Summing the two mutually-exclusive outcomes, we find

$$P(\|k\| = 1) = 2^{-n} + 2^{-n} = 2^{-n+1}$$

consistently with the asymptotic distribution $\|k\| - 1 \sim \mathcal{B}(n-1, 1/2)$. This approach can be extended by computing the probability that a given species i excludes κ_i other species; by summing across all combinations we can approximate the distribution of coexisting species (see Miller *et al.*, SI section B).

4.7 References and further readings

The original metapopulation model:

- Levins, R., 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the ESA, 15(3), pp.237-240.

Many authors contributed to the study of the model with competition-colonization tradeoff:

- Hastings, A., 1980. Disturbance, coexistence, history, and competition for space. Theoretical population biology, 18(3), pp.363-373.

derived the model by extending Levins' model to n populations. Noted that better competitors need to be poor colonizers to yield coexistence.

- Tilman, D., 1994. Competition and biodiversity in spatially structured habitats. Ecology, 75(1), pp.2-16.

performed a thorough analysis of the model, inspired by data on grasslands as well as life-history theory. Noted that infinitely many species could coexist, and derived conditions for limiting similarity.

- Nowak, M.A. and May, R.M., 1994. Superinfection and the evolution of parasite virulence. Proceedings of the Royal Society of London. Series B: Biological Sciences, 255(1342), pp.81-89.

derived the model in the context of superinfection (better pathogens displace others in infected individuals). Showed that this would lead to the coexistence of pathogens of different virulence, rather than convergence to an optimum.

- Kinzig, A.P., Levin, S.A., Dushoff, J. and Pacala, S., 1999. Limiting similarity, species packing, and system stability for hierarchical competition-colonization models. The American Naturalist, 153(4), pp.371-383.

studied the model in the high-diversity limit. Highlighted pathological behaviors of the model. Provided a construction to pack infinitely many species in a finite interval of colonization rates (requires fine-tuning).

- Miller, Z.R., Clenet, M., Della Libera, K., Massol, F. and Allesina, S., 2024. Coexistence of many species under a random competition–colonization trade-off. Proceedings of the National Academy of Sciences, 121(5), p.e2314215121.

contains the derivations presented here, and much more.